Response of Pearly-eyed Thrashers to two intense Hurricanes in the Luquillo Mountains, Puerto Rico

By

ALBERTO C. CRUZ MENDOZA

Thesis submitted to the:

Department of Environmental Sciences, College of Natural Sciences
University of Puerto Rico, Rio Piedras Campus

In partial fulfillment of the requirement for the degree of

MASTER'S IN SCIENCES

In the subject of
ENVIRONMENTAL SCIENCES

23 June 2022
San Juan, Puerto Rico

Response of Pearly-eyed Thrashers to two intense Hurricanes in the Luquillo Mountains, Puerto Rico

By

ALBERTO C. CRUZ MENDOZA

Thesis submitted and accepted by:

Department of Environmental Sciences, College of Natural Sciences

University of Puerto Rico, Rio Piedras Campus

THESIS COMMITTEE

Joseph Wunderle Jr., Ph.D., -Advisor

Frank Rivera Milan, Ph.D.

Jess Zimmerman, Ph.D.

T. Mitchell Aide, Ph.D.

Dedication

I dedicate this thesis to all the people who in a certain way pushed me to continue my graduate career. Here I must mention my two wonderful advisors from my undergraduate studies in the University of Puerto Rico in Humacao Campus, Neftalí Ríos López and Iris Velazquez, for their guidance in my early steps in this research area. Also, to my parents Adalberto Cruz and Rosalyn Mendoza who gave me all their support to archive this goal. Finally, to the person who is my source of motivation to continue this journey, my beloved son Janyel A. Cruz Delgado.

Table of Contents

General Abstract

Hurricanes may have direct and indirect impacts driving changes in forest structure and productivity, thereby altering local avian species richness, abundance, or density. After hurricanes, birds may shift sites in response to vegetation damage or changes in resource availability. The Pearly-eyed Thrasher (*Margarops fuscatus*; thrasher hereafter) is recognized as a "supertramp" because of its high dispersal ability, aggressive behavior, and opportunistic diet, which facilitates colonization of vacant niches in disturbed habitats. Consistent with the supertramp concept, are previous studies indicating that the abundance of thrashers increased in storm-damaged sites after hurricanes. Therefore, I expected thrasher site occupancy and abundance to increase in the most damaged sites in the year (2018) after the passage of the 2017 hurricanes Irma and Maria in the Luquillo Experimental Forest in Puerto Rico. Studies here after the hurricanes indicated that the storm damage to the vegetation increased with elevation, and therefore, I predicted that thrasher site occupancy and abundance would increase with elevation. To test this hypothesis, I used historical point count data of thrashers for the pre-hurricane baseline (1998, 2005) for comparison with post-hurricane point counts conducted at similar sites along the elevation gradient in 2018. During April-August 2018, teams of two observers sampled 158 georeferenced points, which were visited three times each (April-May; June-July; July-August) to sample thrashers. Thrasher site occupancy was estimated with a single-season model and site abundance was estimated with an *N*-mixture model. In the first chapter, I used elevation, forest type, a two-category subjective assessment of hurricane damage at each point count site and year as the covariates for the models. In the second chapter, I

included the Normalize Difference Vegetation Index (NDVI) derived from satellite imagery as a measure of storm damage at each point count site. In addition to covariates of elevation and forest type gathered at each point count site, I used the Mean Information Gain Index (MIG), Green Index (ExG-ExR), and the Leaf Area Index (LAI) as forest structure covariates.

In the first chapter, analyses of detectability suggest that thrasher breeding was delayed and curtailed in the first breeding season after the hurricanes, as demonstrated previously after other hurricanes. My results indicate a decline in thrasher site occupancy and abundance from 1998 to 2005. However, more recently published findings from 2015 indicate that thrasher site occupancy did not continue to decline after 2005 until after the 2017 hurricanes. Although overall thrasher site occupancy and abundance declined from 2005 values after the hurricanes, thrasher site occupancy and abundance in 2018 remained highest at mid-elevation (400-800 m) sites, consistent with pre-hurricane studies. I found no evidence for a shift in thrasher site occupancy and abundance after the hurricanes.

In the second chapter I found a positive relationship between sierra palm cover with thrasher site occupancy and abundance, which is consistent with the importance of sierra palm fruit in the thrasher diet. Also, I demonstrated that NDVI per site showed a negative linear relationship with elevation corroborating previous findings that vegetation damage was greatest at high elevations. In contrast to my predictions, however, thrashers at high elevations (> 600 m) had a higher probability of occupying sites with minimal or no storm damage (as indicated by NDVI values) than more heavily damaged sites in 2018. These heavily damaged sites may have had lower fruit

abundance than less damaged sites as suggested by my field observations. Thrashers may delay colonization of damaged sites at high elevation because of the slow plant regrowth there which retards fruiting. Despite post-hurricane site occupancy and abundance declines in the first year after the hurricanes, the thrasher continues to be a potential threat as a predator and competitor of endangered wildlife at mid-elevation forests in the Luquillo Experimental Forest.

List of Tables

Supplementary Table 1.1. Model selection results of detection probability sub-models with a single-season occupancy model and a single-season n-mixture model analysis. Model selection based on Akaike's Information Criterion (AICc), number of parameters (K), the difference in AICc from the best fit model (ΔQAICc), model weight (AICc.Wt). AICc is the Akaike's Information Criterion value for small sample sizes, which measures the fit of a model relative to other models. Quasi- Akaike's Information Criterion (QAICc) was used when there was an overdispersion in the global model.

Supplementary Table 2.1. Mean predicted estimates values of detection probability (P) across the years and visits. Included the standard error (SE) and the 95% confidence intervals (Lower and Upper).

Supplementary Table 3.1. Model selection result of occupancy probability (Ψ). Covariates considered was elevation, forest type (Tabonuco, Palo Colorado, Sierra Palm, and Elfin Forest), hurricane damage, and years. Included the linear and quadratic term for elevation and forest type. Model selection based on Quasi-Akaike's Information Criterion (QAICc), number of parameters (K), the difference in QAICc from the best fit model (ΔAICc), model weight (QAICc Wt.). AICc is the Akaike's Information Criterion value for small sample sizes, which measures the fit of a model relative to other models. Models for detection (p) were fixed without covariables (.). We assumed constant detection (p[.]) and did not include detection covariates in occupancy models.

Supplementary Table 4.1. Mean predicted estimate values of occupancy probability (Ψ) across the years. Included are the standard error (SE) and the 95% confidence intervals (Lower and Upper).

Supplementary Table 5.1. Model selection result of abundance (λ). Covariates considered were elevation, forest type (tabonuco, palo colorado, sierra palm, and elfin forest), hurricane damage, and years. Also included are the linear and quadratic terms for elevation and forest type. Model selection was based on Akaike's Information Criterion (AICc), number of parameters (K), the difference in AICc from the best fit model (ΔQAICc), model weight (AICc.Wt). AICc is the Akaike's Information Criterion value for small sample sizes, which measures the fit of a model relative to other models. Models for detection (p) were fixed without covariables (.). We assumed constant detection (p[.]) and did not include detection covariates in abundance models.

Supplementary Table 6.1. Mean predicted estimate values of abundance (λ) across the years. Included the standard error (SE) and the 95% confidence intervals (Lower and Upper).

Table 1.2. Model selection results for Pearly-eyed Thrasher site occupancy probability (Ψ) in the year after Hurricane María in the Luquillo Experimental Forest. Model covariates considered were NDVI, elevation, sierra palm Forest, LAI, and MIG. Also, included were some interactions with biological relevance as well as the linear and quadratic terms for elevation and forest type. Model selection was based on Akaike's Information Criterion (AICc), number of parameters (K), the difference in AICc from the best fit model (ΔAICc), model weight (AICc Wt.). AICc is the Akaike's Information

Criterion value for small sample sizes, which measures the fit of a model relative to other models. See Table 1 for code names in models.

Table 2.2. Model selection results for Pearly-eyed Thrasher site abundance (λ) in the Luquillo Experimental Forest in the year after Hurricane María. Covariates considered were NDVI, elevation, sierra palm Forest, LAI, and MIG. Also included were some interactions with biological relevance. Model selection was based on Akaike's Information Criterion (AICc), number of parameters (K), the difference in AICc from the best fit model (∆AICc), model weight (AICc Wt.). AICc is the Akaike's Information Criterion value for small sample sizes, which measures the fit of a model relative to other models. See Table 1 for code names in models.

Supplementary Table 1.2. Camara settings

Supplementary Table 2.2. Pairwise correlation of all covariates for abundance and occupancy sub-models.

Supplementary Table 3.2. Forward stepwise selection for detection probability in single season occupancy model.

Supplementary Table 4.2. Forward stepwise selection for detection probability in single season *N*-mixture model.

Supplementary Table 5.2. Covariate selection for occupancy probability sub-model in single season occupancy model.

Supplementary Table 6.2. Covariate selection for abundance sub-model in single season N-mixture model.

Supplementary Table 7.2. Detection probability beta estimates, standard errors, and p-values from the top ranked model (see Table 1.2 and 2.2).

Supplementary Table 8.2. Predicted values, standard errors, and the 95% confidence intervals (CI) from the top ranked model (see Table 1.2 and 2.2).

List of Figures

Figure 4.2. Pearly-eyed Thrasher predicted site occupancy probability (A) and abundance (B) values across the elevation gradient in the Luquillo Experimental Forest in the year after Hurricane Maria. Red represents low NDVI values (0 – 0.4) and green represents high NDVI values (0.4 – 0.8). Sites with high NDVI values indicate less storm damage to vegetation than sites with low NDVI values.

Supplementary Figure 1.2

Photo description based on the inclination of the camara, 0° for mean information gain and greenness index, and 45° for the leaf area index.

General Introduction

Natural disturbance has the potential to influence ecosystems, community

dynamics and biological cycles in different ways (Pickett et al. 1989). For

example, disturbance agents like storms and fires can make new resources

available for varying life forms, encouraging different dynamics such as the

arrival of new species, thus causing competition, coexistence, and an overall

change in the community structure (Dornelas 2010). Disturbances including

hurricanes, droughts, and sea level rise are predicted to increase in frequency

and intensity over time due to global climate change (Webster et al. 2005,

Knutson et al. 2010). Recent research has shown that these model predictions

are becoming more accurate (e.g., an increase in North Atlantic storms since the

1970s; IPCC 2014). Hurricane disturbances can affect ecosystems and

community dynamics in different ways due to their intense winds and heavy rain

(Walker et al. 1991). Changes in the environment, such as those caused by

hurricanes, influence population processes and affect population densities

(Ricklefs 2000). For example, hurricanes are important factors in some regions

such as the Caribbean by influencing the structure and species composition of

biotic communities because of their frequency and intensity (Walker et al. 1991,

Zimmerman et al. 1996).

Hurricanes effects on birds

For birds, hurricanes may have direct and indirect impacts (Wiley and

Wunderle 1993, Wunderle 1995). Although direct mortality from hurricanes may

reduce many avian populations, it is the indirect effects which may have the

longest lasting effects on bird populations, due to changes in food resources and habitat alterations (Wunderle 1995). These hurricane-derived changes to habitats include defoliation of trees, breakage of tree limbs and trunks, and uprooting of trees (Walker 1991a, 1991b, Greenberg and McNab 1998). Changes in forest structure and productivity can influence availability of foraging substrates, food supplies, nest or roost sites, predation vulnerability, and change microclimates (Wiley and Wunderle 1993, Wunderle 1995). These changes may alter the local avian species richness, abundance, or density (Askins and Ewert 1991, Wauer and Wunderle 1992). However, responses of birds to hurricane impacts may be species-specific (Rittenhouse 2010) and some species can benefit from these disturbances (Greenberg and Lanham 2001, Tejeda-Cruz and Sutherland 2005). For example, some studies indicate that birds that feed on fruit, seeds, or nectar, are more susceptible to population declines than insectivores, omnivores, and predaceous birds after a hurricane impact (Askins & Ewert 1991, Lynch 1991, Waide 1991, Wunderle et al. 1992, Wiley & Wunderle 1993, Wunderle 1995, Lloyd et al. 2019).

Pearly-eyed Thrasher

The Pearly-eyed Thrasher (PETH, *Margarops fuscatus*) is a relatively long-lived species with a wide geographical distribution (Arendt 2006). This species has the potential to adapt to many different habitats, especially in noncompetitive situations (Arendt 2006). The thrasher has been described as an avian super-tramp, which indicates that it that can disperse and colonize human inhabited islands and disturbed habitats (Arendt 2006). This species possesses a

large body, which gives it an advantage over its interspecific competitors when it comes to physical combat over food resources and nesting sites, allowing it to dominate other species for resources (Arendt 2006). Although it is a strong competitor in terms of its versatility in colonizing a diversity of habitats (Arendt 2006), it does not have the capacity to establish itself in a species-rich community of specialist bird species where niches are delineated by diffuse interspecific competition (Faaborg and Chaplin 1988, Terborgh and Faaborg 1980). However, when a major disturbance, such as a hurricane, causes habitat degradation and bird densities decline, the opportunistic and omnivorous thrashers may increase in abundance (Waide 1991, Lloyd et al. 2019) and detection rates after the impact (Wunderle 1995). Although this immediate advantage may last only a short time, before populations of the other bird species recover (Waide 1991) and the foliage returns (Wunderle 1995, Lloyd et al. 2019). In contrast, other studies found declines in thrasher populations shortly after Hurricane Hugo, on St. John, USVI (Askins and Ewert 1991). These different results may be related to the time in which surveys were made after the hurricanes. In tabonuco forest in El Verde, PETH population showed high abundances and capture rates in the first four months after the impact (Waide 1991, Wunderle 1995).

Research Importance

Knowledge of the habitat characteristics at local and landscape scales in relation to abundance and occupancy probability of birds in LEF is important for species-specific management. This is especially important for a predaceous

species such as the PETH which can negatively affect the populations of lizards, frogs, and forest birds, including several threatened and endangered species, including the Puerto Rican Parrot (Arendt 2006). The Puerto Rican Parrot (PRPA) is a critically endangered species (US Fish & Wildlife Service 1999, IUCN 2004), which is threatened by nest competition and predation by the PETH (Snyder et al. 1987). Despite intensive management efforts to increase the reproductive success of PRPA, the competition for nest sites and predation of parrot nests by PETH continues in the LEF (Arendt 2000, 2006, White et al. 2014). I expect that thrasher threats (e.g., competition for nest cavities; predation of eggs or chicks) for the parrot will likely increase in some sites in the LEF with predicted increases in PETH populations in hurricane-damaged sites. Given the PETH threat(s) to the parrot and other sensitive species it will be valuable for managers to know the habitat characteristics of high density PETH sites in the LEF to facilitate management efforts.

Literature Cited

Askins, R.A., and D.N. Ewert. 1991. Impact of Hurricane Hugo on bird populations on St. John, US Virgin Islands. Biotropica 23:481–487.

Arendt, W.J. 2000. Impact of nest predators, competitors, and ectoparasites on Pearly-eyed Thrashers, with comments on the potential implications for Puerto Rican Parrot recovery. Ornitologia Neotropical 11:13-63.

Arendt, W.J. 2006. Adaptations of an avian supertramp: distribution, ecology, and life history of the pearly-eyed thrasher (*Margarops fuscatus*). *US Department of Agriculture, Forest Service, International Institute of Tropical Forestry, Gen. Tech. Rep. 27*.

Dornelas, M. 2010. Disturbance and change in biodiversity. Philosophical Transactions of the Royal Society B: Biological Sciences 365:3719–3727.

Faaborg, J., and S.B. Chaplin. 1988. *Ornithology: An Ecological Approach: Laboratory Manual and Field Exercises*. Prentice-Hall.

Greenberg, C.H., and J.D Lanham. 2001. Breeding bird assemblages of hurricane-created gaps and adjacent closed canopy forest in the southern Appalachians. Forest Ecology and Management 154:251-260.

Greenberg, C.H., and W.H. McNab. 1998. Forest disturbance in hurricane-related downbursts in the Appalachian Mountains of North Carolina. Forest Ecology and Management 104:179-191.

IPCC. 2014. *Climate Change: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Core Writing Team, Pachauri, R.K., and L.A. Meyer.]. IPCC, Geneva, Switzerland, 151 pp.

IUCN 2004. IUCN Red List of Threatened Species. IUCN, Gland, Switzerland [http://www.redlist.org, accessed 23 May 2005]

Knutson, T.R., J.L. McBride, J. Chan, K. Emanuel, G. Holland, C. Landsea, I. Held, J.P. Kossin, A.K. Srivastava, and M. Sugi. 2010. Tropical cyclones and climate change. Nature Geoscience 3:157–163.

Lloyd, J.D., C.C. Rimmer, and J.A. Salguero-Faría. 2019. Short-term effects of hurricanes Maria and Irma on forest birds of Puerto Rico. PLoS ONE 14: e0214432. https://doi.org/10.1371/journal.pone.0214432

Lynch, J.F. 1991. Effects of Hurricane Gilbert on birds in a dry tropical forest in the Yucatan Peninsula. Biotropica 23:488–496.

Pickett, S.T.A., J. Kolasa, J.J. Armesto, and S.L. Collins. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos 54:129–136

Ricklefs, R.E. 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. The Condor 102:9-22.

Rittenhouse, C.D., A.M. Pidgeon, T.P. Albright, P.D. Culbert, M.K. Clayton, C.H. Flather, and V.C. Radeloff. 2010. Avifauna response to hurricanes: Regional changes in community similarity. Global Change Biology 16:905–917.

Snyder, N.F.R., J.W. Wiley, and C.B. Kepler. 1987. The parrots of Luquillo: natural history and conservation of the Puerto Rican parrot. Los Angeles, CA: Western Foundation of Vertebrate Zoology. 384 p.

Tejeda-Cruz, C., and W.J. Sutherland. 2005. Cloud forest bird responses to unusually severe storm damage. Biotropica 37:88–95.

Terborgh, J.W., and J. Faaborg. 1980. Saturation of bird communities in the West Indies. The American Naturalist 116:178-195.

USFWS (US Fish & Wildlife Service). 1999. Technical/Agency Draft Revised Recovery Plan for the Puerto Rican Parrot (*Amazona vittata*). USFWS Region 4, Atlanta, USA.

Waide, R.B. 1991. The effect of Hurricane Hugo on bird populations in the Luquillo experimental forest, Puerto Rico. Biotropica 23:475-480.

Walker, L.R. 1991a. Summary of the effects of Caribbean hurricanes on vegetation. Biotropica 23:442-447.

Walker, L.R. 1991b. Tree damage and recovery from Hurricane Hugo in Luquillo experimental forest, Puerto Rico. Biotropica 23:379-385.

Wauer, R.H., and J.M. Wunderle Jr. 1992. The effect of Hurricane Hugo on bird populations on St. Croix, US Virgin Islands. Wilson Bulletin 104:656–673.

Weaver, P.L. 1986. Hurricane damage and recovery in the montane forests of the Luquillo Mountains of Puerto Rico. Caribbean Journal of Science 22:53-70.

Webster, P.J., G.J. Holland, J.A. Curry, and H.R. Chang. 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. Science 309:1844–1846.

White Jr, T.H., J.A. Collazo, S.J. Dinsmore, and I. Llerandi-Román. 2014. Niche restriction and conservatism in a Neotropical psittacine: the case of the Puerto Rican Parrot. *Habitat loss: causes, effects on biodiversity and reduction strategies.* Nova Science 1-83.

Wiley, J.W., and J.M. Wunderle Jr. 1993. The effects of hurricanes on birds, with special reference to Caribbean islands. Bird Conservation International *3*:319-349.

Wunderle Jr, J.M. 1995. Responses of bird populations in a Puerto Rican forest to Hurricane Hugo: the first 18 months. Condor 879-896.

Wunderle Jr, J.M., D.J. Lodge, and R.B. Waide. 1992. Short-term effects of Hurricane Gilbert on terrestrial bird populations on Jamaica. The Auk 109:148–166.

Zimmerman, J. K., M.R. Willig, L.R. Walker, and W.L. Silver. 1996. Disturbance and Caribbean ecosystems. Biotropica 28:414-423.

Chapter 1: Effects of Hurricanes Irma and María on Abundance and Occupancy of Pearly-eyed Thrashers in the Luquillo Experimental Forest, Puerto Rico

Alberto C. Cruz-Mendoza[a]*, Laura L. Fidalgo-De Souza[a], Frank F. Rivera-Milán[b], Jessica Ilse[c], Wayne J. Arendt[c], & Joseph M. Wunderle, Jr.[a,c]

[a] Department of Environmental Science, University of Puerto Rico, Rio Piedras, PR 00931

[b]Division of Migratory Bird Management, United States Fish and Wildlife Service, 11510 American Holly Drive, Maryland 20708, USA

[c] International Institute of Tropical Forestry, USDA Forest Service, Sabana Field Research Station, HC 02 Box 6205, Luquillo, Puerto Rico 00773, USA

Abstract

The Pearly-eyed Thrasher (*Margarops fuscatus*; thrasher hereafter) is recognized as a "supertramp" because of its high dispersal ability, aggressive behavior, and opportunistic diet, which facilitates colonization of vacant niches in disturbed habitats. As a supertramp, the thrashers are expected to shift sites along the elevation gradient after hurricanes Irma and Maria extensively damaged vegetation in September 2017. To document the hurricanes' effects on thrasher site occupancy and abundance in the Luquillo Experimental Forest (LEF), we compared point count results obtained before (1998, 2005) and after the hurricanes (2018). Thrasher abundance was estimated with an *N*-mixture model and occupancy was estimated with a single-season model, with year as a covariate in all models. Elevation (with a quadratic effect) was the most important covariate for site abundance and occupancy estimation. Occupancy across 110 survey sites decreased from 0.77 [0.03 SE] in 1998 to 0.50 [0.03] in 2005 and 0.37 [0.03] in 2018 after the hurricanes. Abundance estimates decreased from an average of 11 [0.75 SE] individuals/site in 1998 to 4.39 [0.37] in 2005 and 2.33 [0.19] in 2018. Occupancy and abundance were highest at mid-elevation (400-800 m) in all years and there was no evidence of a shift in elevation range after the hurricanes in 2018. Despite post-hurricane occupancy and abundance declines, the thrasher continued to be a potential threat as a predator and competitor of endangered wildlife at mid-elevation forests in the LEF.

Keywords – Abundance, Hurricanes, Occupancy, *Margarops fuscatus*

Introduction

The Caribbean has a high frequency of tropical cyclones, including tropical storms and hurricanes (Walker et al. 1991). These tropical cyclones (hurricanes hereafter) can have major effects on ecosystem structure and function and may occur with sufficient frequency to play an important role in structuring biotic communities (Odum and Pigeon 1970, Walker et al. 1991, Zimmerman et al. 1996). In 2017, the Atlantic had a very active season with two major hurricanes affecting Puerto Rico. Hurricane Irma passed ~80 km northeast of the island on 6 September as a Category 5 (Saffir-Simpson scale) with wind speeds approaching 300 km/h. On 20 September, Hurricane Maria made landfall on southeastern Puerto Rico and crossed diagonally over the island exiting on the northwest coast as a Category 4 storm with maximum sustained winds of ~250 km/h. Hurricane Maria was the most intense hurricane recorded in Puerto Rico for almost ninety years, after Category-5 Hurricane San Felipe II in 1928 (Garcia-Rivera et al. 2018). Compared to Category-3 Hurricane Hugo in 1989, vegetation damage caused by Hurricane Maria tripled stem breakage and doubled tree deaths (Uriarte et al. 2019).

We expected these hurricanes to have both direct and indirect effects on bird populations (Wiley and Wunderle 1993). Although direct mortality from hurricanes may cause occupancy and abundance declines, it is the indirect effects that may have the longest-lasting effects on bird populations, due to changes in food resources and habitat alterations (Wiley and Wunderle 1993, Wunderle 1995). Previous studies indicate that birds that feed on fruit, seeds or

nectar are more susceptible than are insectivores, omnivores, and carnivore birds (Askins and Ewert 1991, Lynch 1991, Waide 1991, Wunderle et al. 1992, Wiley and Wunderle 1993, Wunderle 1995, Lloyd et al. 2019). However, responses of some birds to hurricanes may be species-specific (Rittenhouse 2010, Lloyd et al. 2019) and certain species may, in the long term, benefit from these disturbances (Tejeda-Cruz and Sutherland 2005, Lloyd et al. 2019, Campos-Cerqueira and Aide 2021).

A species that is expected to benefit over the long-term from hurricanes is the Pearly-eyed Thrasher (*Margarops fuscatus,* thrasher hereafter), which has the potential to adapt to different habitats, especially in depauperate or non-competitive situations as evident in its widespread geographical and elevational distribution in the Caribbean (Arendt 2006). The thrasher has been described as an avian supertramp because it can disperse widely and colonize human-inhabited islands and disturbed habitats with few potential competitors (Arendt 2006). The species is an opportunistic forager as evident by its omnivorous diet composed of a wide variety of foods including large insects, bird eggs and nestlings, lizards, frogs, and a variety of fruits (Arendt 2006), and even rodents (Rollé 1965). The thrasher possesses a relatively large body, which gives it an advantage over its smaller competitors when it comes to physical combat over food resources and nesting sites, allowing it to dominate other species for resources (Arendt 2006). As a competitor and predator, the thrasher is a threat to endangered species including various species of frogs, lizards, and birds. The thrasher is a species of concern for managers of the endangered Puerto Rican

Parrot (*Amazona vittata*) because of its competition for nest cavities and depredation of eggs and nestlings (U.S. Fish and Wildlife Service 1999, IUCN 2004, Snyder et al. 1987).

Given the thrasher's opportunistic diet, dispersal ability and colonization of species-poor habitats, we expected a post-hurricane shift in habitats or sites occupied in response to vegetation damage. Several studies have documented shifts in habitat, sites, or elevation after hurricanes by various bird species (Arendt 2000, Wunderle et al. 1992, Wunderle 1995) including post-hurricane site shifts by Pearly-eyed Thrashers (Askins and Ewert 1991, 2020; Wunderle 1995). Some post-hurricane site shifts by birds are believed to be associated with resource or habitat differences in resistance to storm damage or recovery rates (Wiley and Wunderle 1993). Birds with broad elevational distributions, such as the thrasher, might be expected to show post-hurricane elevational shifts as they respond to elevational gradients in storm damage or vegetation recovery. Site shifts in the thrasher's elevational distribution in the Luquillo Mountains (100 to 1075 m) of eastern Puerto Rico following Hurricane Maria were expected as a result of the higher storm damage to vegetation at higher elevations (Hu and Smith 2018, Feng et al. 2020) and the likelihood of slower recovery rates typical of high elevation vegetation (Weaver 1990, Walker et al. 1996). Therefore, after Hurricane Maria we expected the thrashers to move from their preferred mid elevation Palo Colorado Forest (Pagan 1995, Arendt 2006, Campos-Cerqueira et al. 2017) to other forest types or elevations.

The objective of this study was to quantify the effects of the 2017 hurricanes on thrasher site occupancy and abundance relative to baseline surveys in 1998 and 2005 along the elevation gradient in the Luquillo Mountains. We designed the study to test the hypothesis that thrasher site occupancy and abundance in 2018 would change with elevation, forest type, and vegetation damage. Results from this study are relevant for understanding the response and resilience of an avian Supertramp to a major hurricane, and for the conservation of endangered species threatened by the thrashers.

Methods

Field-site Description

The study was conducted in the Luquillo Experimental Forest (also known as El Yunque National Forest) in northeastern Puerto Rico (Fig. 1). The Luquillo Experimental Forest (LEF) has been well studied by ecologists (Harris et al. 2012) and is the largest protected area (115 km²) with primary forest in Puerto Rico (Lugo 1994). The LEF includes most of the Luquillo Mountains which have a maximum elevation of 1074 m a.s.l. and have a strong effect on abiotic factors (temperature, rain, humidity), and the biota (Weaver and Gould 2013). The temperature differs by 7°C for mean maximum values between low and high sites but annually varies little with elevation for mean monthly temperatures (3-3.5 °C). Annual rainfall ranges from an average of 2450 mm/yr in the lowlands to 4000 mm/yr at higher elevations. The LEF has five ecological life zones: subtropical moist forest, subtropical wet forest, subtropical rainforest, lower montane wet forest, and lower montane rain forest (Ewel and Whitmore 1973), as well as four main forest types (Wadsworth 1951). The main forest types includes: (1) the tabonuco forest which is dominated by *Dacryodes excelsa* V. (Candlewood or Tabonuco) and occurs between 150 and 600 m, most commonly in the subtropical moist and wet forests; (2) the palo colorado forest which is dominated by *Cyrilla racemiflora* L. (Swamp titi or Palo Colorado) and occurs between 600 and 950 m, most commonly in the lower montane wet and rainforests; (3) the elfin forest which is dominated by *Tabebuia rigida* Urb. (Roble de Sierra) and *Eugenia borinquensis* B. (Guayabota de Sierra), occurring above 950 m and

16

most commonly in the lower montane rain forest; and (4) the sierra palm forest which is dominated by *Prestoea acuminata var. montana* G. (Sierra Palm or Palma de Sierra) and occurs anywhere interspersed between the elfin and palo colorado forests. The sierra palm forest or palm brake is mostly found on steep slopes at higher elevations.

Bird Surveys

Pre-2017. Thrasher surveys were conducted along the elevation gradient in the LEF using the fixed-radius point count method of Hutto et al. (1986) by Arendt and assistants from 1989 to 2006 (Arendt et al. 2013). For the purpose of this research, however, we only used data from 1998 and 2005. We used data from these two years because of the absence of hurricanes, as well as to allow time (>6 yr) for recovery from Hurricane Hugo in September 1989 and Georges inSeptember 1998. In addition, counts in both 1998 and 2005 occurred during April–August, coinciding with the post-hurricane survey period of 2018. With few exeptions, surveys during the 17-year period were conducted every month (Arendt 2006). These surveys included 130 georeferenced points separated by a minumum distance of 100 m and located along six trails or roads within the LEF: East Peak (15 points), Mt. Britton (15), Icacos (30), Palo Hueco (30), Catalina (10), and Route 988 (30). However, in 1998 there were only 80 points available because the Route 988 points was established in 1999 after Hurricane Georges. In 2005, we surveyed 110 points to match those available in 2018 (see below). At each point, a single observer recorded thrasher audio and visual detections

during 10 minutes between 05:00 to 10:30 hours, and estimated detection

distance to single individuals or cluster center (Thomas et al. 2010).

Post-2017 – During April-August 2018, we surveyed the same 110 points

of 2005 (Arendt 2006), three times between 05:30 and 11:30 hours. We did not

surveys 20 of the original 130 points due to inaccessibility after the 2017

hurricanes. The 2018 surveys differed from those conducted in 1998 and 2005,

because we used a team of two observers instead of one, with one observer

recording the data and the other measuring detection distances (Burnham et al.

2004, Rivera-Millan et al. 2014). Distances to single thrashers or clusters were

measured with a laser rangefinder (Rivera-Millan et al. 2014), which provides

more precision that the visual estimates of Arendt (2006). We defined a cluster

as two or more birds within 10 m of each other. Nonetheless, when vocalizing

birds could not be visually detected, we measured distances to the nearest

horizontal location and grouped detections using the following distance

categories: 0–5, 6–15, 16–25, 26–50, 51–75, 75–100, and 100 < m. Based on

the distances measured, we truncated the count data at 50 m and define an area

of 0.79 ha (~0.01 km^2) for occupancy and abundance estimations.

Occupancy and Abundance modeling

We used single-season occupancy models (MacKenzie et al. 2002, Fuller

et al. 2016) to estimate detection probability (p) and occupancy (ψ) and explore

the influence of survey-specific and site-specific covariates in 1998, 2005 and

2018. In addition, we used *N*-mixture models (Royle 2004) as adapted by Nareff

et al. (2019) and Fuller et al. (2016) to estimate detection and abundance

(lambda [λ] per survey point and across survey points). This method assumes

constant occupancy and abundance (i.e., population closure to births, deaths,

immigration, or emigration between survey occasions during April-Agust 2018),

which allowed us to estimate occupancy and abundance assuming count

independence between points surveyed each year in 1998, 2005, and 2018

(Fuller et al. 2016, Nareff et al. 2019). Thus, we fitted and compared occupancy

and *N*-mixture models that combined data from the point-count surveys of 1998,

2005, and 2018.

The detection model included the covariates year, ordinal date of the

survey (date), start time of the survey (time), and level of hurricane damage.

Hurricane damage class was estimated by the observer in the first visit from the

center of each point count site and involved two categories: 1= medium to high

damage, 0 = no to light damage. We modeled abundance and occupancy

probability as a function of the following covariates: elevation above sea level,

percent cover of four main forest types (i.e., % tabonuco, % palo colorado, %

sierra palm, and % elfin forest) within a 50-meter radius, year of survey, and

hurricane damage class (only for year 2018). We used the quadratic effect for

elevation and forest type because previous studies have documented quadratic

responses of thrasher distribution along the elevational gradient of the LEF, and

the covariance of forest types with elevation (Arendt 2006, Campos-Cerqueira et

al. 2017). All numeric covariates were re-scaled to a mean and standard deviation (SD) of 0 and 1 respectively.

For each surveyed point, we measured elevation and forest composition using freely available raster layers. Elevation data were directly acquired from the USGS Digital Elevation Model (DEM) data at a 1 m resolution (Gesh and Maune 2007). For the forest composition, we established a grid of 3,891 hexagons of 31,000 m^2 over a map of the LEF and the percent of vegetation cover of each forest type using the Puerto Rico GAP Analysis raster layer (Gould et al. 2008). Values for elevation and percentage of each forest type were extracted from the cell values of the specific site covariate raster-based layers on the set of survey points and recorded to an attribute table of the output GIS vector layer.

Model Selection

We used a multi-stage model fitting approach for 23 potential models (Karanth et al. 2011, Fuller et al. 2016, Nareff et al. 2019). Our analyses differ from those of Fuller et al. (2016) and Nareff et al. (2019) by using a secondary candidate set strategy that fits sub-models independently and combines the top set models from each sub-model for selection in the final stage (Bromaghin et al. 2013, Morin et al. 2020). We used R package 'UNMARKED' (Fiske and Chandler 2011) in R version 4.0.5 (R Core Team 2021) for model fitting. First, we assessed the goodness-of-fit of the global model and calculated the overdispersion parameter (ĉ) before evaluating the possible combinations of covariates to select best models for occupancy and abundance. This

overdispersion parameter was used to calculate the Quasi-Akaike's Information

Criterion (QAIC) for model selection using the AICcmodavg package (Mazerolle

2020), which is standard practice for dealing with lack-of-fit (Kéry and Royle

2016). In the case where the ĉ was close to one, we did not use the QAIC. We

calculated the effective sample sizes (n-*ess*) to obtain the corrected Akaike's

Information Criterion (AICc).

We started our modeling process by choosing the best detection

probability model. For this we separately fitted one factor models with covariates

including year, hurricane damage, date, and time of day, and then fitted two-

factor additive models that included year + hurricane damage, year + date, and

year + time, thus yielding seven candidate models for thrasher detection (Table

S1). This was followed by selecting the best occupancy and abundance models

from the set of seven models. For this we again fitted one-factor models for

covariates year, hurricane damage, elevation, and each of the four forest types:

% tabonuco, % palo colorado, % elfin forest, and % sierra palm. We then created

two-factor additive models combining year with each of the other six covariates.

This was repeated with the quadratic forms of the covariates elevation and the

four types of percent forest cover. This yielded a total of 23 candidate models

each for occupancy and abundance (Tables S1, S2, S3). We compared and

selected best models based on a criterion of Δ AICc ≤ 2. Finally, we plotted the

predicted parameter values of thrasher occupancy and abundance for supported

model covariates to examine the changes in pre- and post-hurricane values.

Results are presented as means with standard errors (SEs) and 95% confidence

intervals (CI), using the predicted values for each point and the two-tailed z score

to estimate them (Charter 1997). We determined statistical difference by lack of

overlap in the 95% CI, but we consider that a < 30% of overlap in the CIs remain

significantly diferent (Van Belle 2002).

Results

We detected 256 thrashers at 65 of 80 points during the 1998 surveys,

107 thrashers at 43 of 110 points during the 2005 surveys, and 47 thrashers at

27 of 110 points during the 2018 surveys. The goodness-of-fit test indicated

overdispersion with $\hat{c}$ = 3.15 (p = 0.008) for the global model of the single-season

occupancy model, and therefore we used this value to calculate the QAIC scores

for subsequent model selection. For the *N*-mixture model, the goodness-of-fit

test ($\hat{c}$ = 0.99; p = 0.45) indicated that there was no overdispersion, which led us

to use AIC. The global model in single-season occupancy and N-mixture model

included covariates year, ordinal date, start time, and hurricane damage in

detection sub-model. And for occupancy and abundance included year, hurricane

damage, elevation, tabonuco, palo colorado, sierra palm, elfin forest, and the

quadratic effect for the last five covariates.

The top detection model included year and ordinal date of the surveys

(Table S1). The β coefficients from the top model for year and ordinal dates

showed a negative slope. However, the confidence intervals (95%) of the

detection estimates indicated that there were differences between visits (dates),

but not between years (Table S2). Thrasher detection probability was similar

during the first survey visit of both pre-hurricane years (1998 and 2005) but

declined after the 2017 hurricanes (1998: 0.70, 95% CI = 0.68-0.73; 2005: 0.70,

95% CI = 0.68-0.72; 2018: 0.55, 95% CI = 0.53-0.58). However, no differences in

detectability were found among the years during the second visits (1998: 0.48,

95% CI = 0.46-0.51; 2005: 0.48, 95% CI = 0.45-0.50; 2018: 0.44, 95% CI = 0.41-

0.47) and during the third visits (1998: 0.27, 95% CI = 0.25-0.29; 2005: 0.28,

95% CI = 0.27-0.30; 2018: 0.27, 95% CI = 0.25-0.29). Overall, mean detectability

for all years declined across the three visits from visit one (0.65, 95% CI = 0.63-

0.67) to visit two (0.47, 95% CI = 0.44-0.47) and visit three (0.27, 95% CI = 0.26-

0.29).

Model selection results for occupancy probability indicated that the best

model included year and elevation with a quadratic term (Table S3.1). The top

model estimates for occupancy probability across sites in each year were (0.77

[0.03 SE], 95% CI = 0.71-0.83) in 1998, (0.50 [0.03], 95% CI = 0.44-0.57) in

2005, and (0.37 [0.03], 95% CI = 0.31-0.43) post-hurricane in 2018. These

values showed difference across all years. The relationship between elevation

and occupancy probability was similar (positive parabolic) across years, but with

different values between years of occupancy probability (e.g., Ψ = a + year -1.1

[0.6] + elevation -0.2 [0.2] + elevation^2 -2.3 [0.3] in Fig. 2A). The highest values

of occupancy probability were in the mid elevations (~400 – 800 m) in the three

years with (0.95 [0.01], 95% CI = 0.94-0.96) in 1998, (0.87 [0.01], 95% CI = 0.86-

0.88) in 2005, and (0.71 [0.01], 95% CI = 0.69-0.72) post-hurricane in 2018

(Table S4.1).

As found for occupancy, model selection results for abundance indicated

that the best abundance model included year and elevation with a quadratic term

(Table S5.1). The top model estimates for the abundance across sites in each

year were (11 [0.75 SE], 95% CI = 9.53-12.46) in 1998, (4.39 [0.37], 95% CI =

3.68-5.11) in 2005, and (2.33 [0.19], 95% CI = 1.95-2.71) post-hurricane in 2018.

These values showed difference across all years as found for occupancy. Also, the relationship between elevation and abundance was the same (positive parabolic) and different across years (e.g., λ = a + year -0.5 [1.5] + elevation 0.7 [0.2] + elevation^2 -1.9 [0.2] in Fig. 2B). Furthermore, as with occupancy, the higher values of abundance were in the mid-elevations (~400 – 800 m) in the three years with (15.83 [0.27], 95% CI = 15.30-16.37) in 1998, (8.40 [0.13], 95% CI = 8.15-8.66) in 2005, and (4.46 [0.08], 95% CI = 4.31-4.61) post-hurricane in 2018 (Table S6.1).

Discussion

Pearly-eyed Thrasher detection probability varied with the covariate ordinal date as expected because thrashers are likely to be easier to detect during their breeding season when they are most vocal, in contrast to their non-breeding period. In the absence of hurricanes, the normal thrasher breeding season in the LEF extends from January to July (Arendt 2006, Beltrán et al. 2010). However, in the first breeding season after a hurricane, nesting may be delayed to April, as documented after hurricanes Hugo and Georges (Arendt 2006). Consistent with post-hurricane delayed nesting was our finding that thrasher detections during the first visit in April – May 2018 were lower than detections during the first visits of the 1998 and 2005 surveys. Also, as documented by Arendt (2006), we found no evidence of increased detections in visits two and three, which would suggest that post-hurricane extended nesting to compensate for delayed breeding. Delayed and reduced nesting activity after hurricanes has been related to vegetation damage and limited food supply, in particular the fruit of sierra palms (Wunderle 1999), which are important for thrasher reproduction (Arendt 2006, Beltrán et al. 2010).

Our pre-hurricane surveys indicated that the LEF thrasher population declined between 1998 and 2005, as evident in a 35% decline per points in occupancy and a 60% decline in abundance. The cause or causes of this decline are unknown (Arendt 2006). Although it is uncertain if the LEF thrasher population continued to decline in site abundance after 2005, thrasher site occupancy as measured by passive acoustic monitoring along the elevation

26

gradient in the LEF in 2015 by Campos-Cerqueira et al. (2017) and in 2016 by

Campos-Cerqueira and Aide (2021) were comparable to our 2005 occupancy

values. For example, our 2005 thrasher site occupancy value (0.50 [0.09 SE]),

was similar to the 2015 value (0.51 [0.11]) and the 2016 value (0.49 [0.11]), even

after a 2015 – 2016 drought. Therefore, we believe that the thrasher population

decline from 1998 to 2005 had ceased in the LEF before the arrival of the 2017

hurricanes, suggesting that our 2005 occupancy and abundance values may

serve as a reasonable baseline for comparison of hurricane effects.

Assuming thrasher average occupancy and abundance estimates were

similar to our 2005 estimates, average occupancy declined by ~26% (i.e., 0.50

occupancy in 2005 to 0.37 in 2018) and abundance declined ~47% (i.e., 4.39

abundance in 2005 to 2.33 abundance in 2018) after the 2017 hurricanes.

Although there are no other pre- vs. post-hurricane studies of thrasher numbers

in the LEF for comparison, we note that annual mortality of breeding thrashers in

the palo colorado forest decreased by 53% in the first breeding season after

Hurricane Hugo (i.e., 89% annual survival in ten non-hurricane years to 42%

annual survival in the first year after Hurricane Hugo, Arendt 2006). The post-

Hugo decline in annual survival suggests that mortality plays an important role

relative to emigration in thrasher population site declines after hurricanes.

Despite uncertainty as to how well post-hurricane decline in thrasher annual

survival (53% after H. Hugo) directly relates to a decline in site abundance (47%

after H. Maria), it appears that the relative magnitude of the post-hurricane

declines was similar. The magnitude of the post-hurricane decrease in thrasher

site occupancy and abundance in the LEF falls within the range of declines recorded in other species after hurricanes elsewhere (e.g., Askin and Ewert 2020, Campos-Cerqueira and Aide 2021)

Despite our finding of an overall decline in thrasher site occupancy and abundance in the LEF from 1998 to 2005 to 2018, the maximum values of these measures for each of these years remained in the 400 to 800 m elevation range. Similarly, Campos-Cerqueira et al. (2017) found that thrasher site occupancy was highest from 450 to 850 m elevations in the LEF, and that the elevation range had contracted from 1998 to 2015 with a significant decrease in site occupancy only in the upper range limit. Maximum site occupancy values for LEF thrashers continued to remain in the 400 to 800 m elevation range in 2016, despite a severe 2015–2016 drought, and in 2019 after two years of recovery from the 2017 hurricanes (Campos-Cerqueira and Aide 2021). Thus, despite overall elevation-wide changes in thrasher site occupancy and abundance, some associated with extreme weather events, thrashers continued to remain most abundant in the mid-elevation wet forest of the LEF. The preference for this elevation zone by the thrasher, a secondary cavity nester, has been attributed to the availability of cavities for nesting in large trees in the palo colorado forest (Arendt 2004) and the proximity of sierra palm forests for fruit (Beltrán et al. 2010).

In contrast to our predictions, we found no evidence for post-hurricane shifts in elevation by thrashers in the LEF, at least in the first year after the 2017 hurricanes. By the second year (2019) after the hurricanes, however, site

occupancy estimates in the LEF indicated that thrashers had shifted further up

the mountain (Campos-Cerqueira and Aide 2021). Several factors likely

contributed to the thrasher movement into higher elevation sites in 2019. For

instance, thrasher reproduction performance may have increased in the second

post-hurricane breeding season after the 2017 hurricanes as occurred after other

storms. For example, in the second breeding season after Hurricane Hugo,

Arendt (2006) found that thrasher breeding was initiated earlier than normal

resulting in an abnormally high number of successive clutches per female,

attributable to increased primary productivity in the second year after the

hurricane (Scatena 1995). This increased reproductive success may have

contributed to thrasher movement into higher elevations. In addition, vegetation

recovery may have been delayed at higher elevations as a result of greater

vegetation damage than at lower elevations after Hurricane Maria (Hu and Smith

2018, Feng et al. 2020) and slower growth rates of vegetation at high elevations

(Weaver 1990, Walker et al. 1996). Slower vegetation recovery at high elevations

may have in turn delayed availability of thrasher food resources, such as fruits,

insects, lizards, and frogs.

Elsewhere, Pearly-eyed Thrashers have shown diverse post-hurricane

population site shifts. For example, and in contrast to our LEF findings, post-

Hurricane Maria thrasher site occupancy significantly increased from baseline

occupancy estimates in mid-to high elevation sites (median = 760 m; range: 5 –

1,297 m) in the Cordillera Central of Puerto Rico in the first year of after the

hurricanes (Llyod et al. 2019). This latter finding may reflect a post-hurricane

increase in thrasher home range size or wandering as thrashers searched more widely for food. Or alternatively, it may represent a habitat or elevational shift by thrashers from elsewhere, possibly from the lowland habitats, which were not well represented in their study. Why our thrasher occupancy results sampled in 2018 in the LEF differ from the 2018 results of Llyod et al. (2019) is unknown, but it should be noted that the LEF was impacted by two hurricanes in contrast to the Cordillera Central which was distant from Hurricane Irma's path and therefore little affected by Irma. Furthermore, the LEF was on the north side of Hurricane Maria, where winds tend to be strongest in contrast to Cordillera Central sites which were situated on Maria's south side where winds generally tend to be weaker.

Other instances of thrasher site or habitat shifts after hurricanes have been documented on other islands. For example, on St. Croix eight months after Hurricane Hugo, thrasher counts increased on one transect and decreased on another (Wauer and Wunderle 1992). On nearby St. John, thrashers declined significantly in dry woodlands but not in moist forests in the year after Hurricane Hugo (Askins and Ewert 1991), but inversely after Hurricane Maria, declined in moist forests and increased in dry woodlands two years after Hurricane Maria (Askins and Ewert 2020). Whether these examples of post-hurricane thrasher site shifts are attributable to differences in habitat suitability (e.g., habitat damage or recovery) or a result of site differences in detectability are unknown. Although these Virgin Island studies did not measure detectability directly, the restriction of counts to within 25 m radius around the observer likely reduced thrasher

30

detectability differences among sites. Post-storm habitat shifts by birds, including

thrashers, may be of short duration and limited spatial scale following a hurricane

as found by Wunderle (1995) in the lowland tabonuco forest of the LEF. Here,

two weeks after Hurricane Hugo both ground level mist net captures (< 2.5 m

above ground) and 25 m fixed-radius point counts of thrashers were

exceptionally high (above baseline pre-hurricane values), but values from both

sampling methods declined to lower levels after four months, and thereafter

remained low and only slightly above baseline values for the duration of the 18-

month study. The increase in mist net captures and point count detections in the

first four months after Hugo were attributed to canopy loss, which resulted in

canopy dwellers, including thrashers, shifting to ground level (< 2.5 m) after the

storm eliminated the canopy. Therefore, post-hurricane Maria thrasher site shifts

in the LEF may have occurred temporarily as canopy-dwelling thrashers adjusted

to canopy loss in the four months prior to our 2018 surveys, or after surveys in

2019 by Campos-Cerqueira and Aide (2021) with expected increases in primary

productivity and thrasher reproductive output.

We found no evidence that our covariates for hurricane vegetation

damage or for forest type were associated with thrasher site occupancy or

abundance after the hurricanes. The absence of covariation of site occupancy or

abundance with hurricane vegetation damage may be attributable to its

subjective assessment by different observers as a categorical covariate where

the value of 0 showed no or little damage and the value of 1 showed medium or

high damage. It is possible that the low precision of this covariate affected its

choice in the models, especially in different forest types. For instance, a heavily

damaged palm forest (score 1) may have suffered little palm tree mortality but

lost most palm fronds, which were replaced quickly thereby closing most of the

palm canopy within a year after the storm. In contrast, a heavily damaged

tabonuco or palo colorado site (score 1) may have suffered some tree mortality

(e.g., trunk snap, wind throw) and loss of major canopy branches thereby

retarding canopy closure for many years.

Our forest type covariate was based on classification into one of four

forest types based on the dominant tree species for each forest type, which may

have obscured changes in plant species composition along the elevation

gradient. There are several weaknesses associated with the use of a forest type

classification scheme to characterize vegetation variation along the elevation

gradient in the LEF as recognized by Heartsill-Scalley (2012). For example,

cloud cover and topography influence the distribution and density of plant

species across the LEF elevation gradient (Silver et al. 1999, Barone et al. 2008).

Even within a forest type or elevation range, differences in topography such as

ridge, slope, or riparian zones differ in plant species composition reflecting

differences in nutrient, moisture, and edaphic conditions (Heartsill-Scalley 2012).

Also, not all plant species covary with the dominant tree species typical of a

forest type along the elevation gradient. Moreover, the forest type classification

does not include differences in plant age, stature, or disturbance history, all of

which may vary within a forest type.

Despite post-hurricane declines in average site occupancy and site abundance, overall thrahser distribution along the elevational gradient was remarkably resistant to the 2017 hurricanes, by maintaining peak values at ~400 – 800 m in the first year (2018) and second-year (2019; Campos-Cerquiera and Aide 2021) following the hurricanes. The thrasher's post-hurricane fidelity to peak abundance in this elevation range, which encompasses palo colorado and palm forest types, suggests that thrasher competition and predation remains a threat to sensitive animal populations in this zone even in the aftermath of hurricanes. Although the palo colorado forest type in this elevation zone has been the focus of Puerto Rican Parrot recovery efforts (i.e., nest cavity provisioning and guarding) since the late 1970s (Snyder et al. 1987, White et al. 2014) management efforts in the LEF now concentrate in lower elevations (~450 m elevation) near the parrot aviary (Thomas White, personal communication). Our findings which indicate thrashers did not shift downward into the lower forests of the LEF in the year after the hurricanes and in the second year after the hurricanes (Campos-Cerquiera and Aide 2021) suggest that the thrasher threat to breeding parrots in the lower elevation remains low even in the aftermath of hurricanes. However, our post-hurricane findings of peak thrasher abundance at mid-elevations in 2018 and the finding of an upward elevation shift in site occupancy by thrashers in 2019 by Campos-Cerquiera and Aide (2021) is of conservation concern for mid to high elevation endangered species such as the populations of *Eleutherodactylus* frogs already under threat from global climate change.

Acknowledgments

Literature Cited

Arendt, W.J. 2000. Impact of nest predators, competitors, and ectoparasites on Pearly-eyed Thrashers, with comments on the potential implications for Puerto Rican Parrot recovery. Ornitologia Neotropical 11:13-63.

Arendt, W.J. 2004. Open- and cavity-nesting traits merge in the evolution of an avian supertramp, the pearly-eyed thrasher (*Margarops fuscatus*). Ornitologia Neotropical 15:455–465.

Arendt, W.J. 2006. Adaptations of an Avian Supertramp: Distribution, Ecology, and Life History of the Pearly-Eyed Thrasher (*Margarops fuscatus*). US Department of Agriculture, Forest Service, International Institute of Tropical Forestry, Gen. Tech. Rep. 27.

Arendt, W.J., S.S. Qian, and K.A. Mineard. 2013. Population declines of the Elfin-woods Warbler (*Setophaga angelae*) in eastern Puerto Rico. Bird Conservation International 23:136-146.

Askins, R.A., and D.N. Ewert. 1991. Impact of Hurricane Hugo on bird populations on St. John, US Virgin Islands. Biotropica 23:481–487.

Askins, R.A., and D.N. Ewert. 2020. Resistance and resilience of Virgin Islands bird populations following severe hurricanes. Wilson Journal of Ornithology 132:898-910.

Barone, J.A., J., Thomlinson, P. A., Cordero, and J. K. Zimmerman. 2008. Metacommunity structure of tropical forest along an elevation gradient in Puerto Rico. Journal of Tropical Ecology 24:525-534.

Beltrán, J.W., J.M. Wunderle, Jr., and W.J. Arendt. 2010. Changes in home
range of breeding and post-breeding male Pearly-eyed Thrashers in the
Luquillo Mountains of Puerto Rico. Ornitologia Neotropical 21:409-423.

Bender, M.A., T.R. Knutson, R.E. Tuleya, J.J. Sirutis, G.A. Vecchi, S.T., Garner,
and I.M. Held. 2010. Modeled impact of anthropogenic warming on the
frequency of intense Atlantic hurricanes. Science 32:454-458.

Bromaghin, J.F., T.L. McDonald, and S.C. Amstrup. 2013. Plausible
combinations: An improved method to evaluate the covariate structure of
Cormack-Jolly-Seber mark-recapture models. Open Journal of Ecology, 3:11-
22.

Brown, S., A.E. Lugo, S. Silander, and L.H. Liegel. 1983. Research history and
opportunities in the Luquillo Experimental Forest. Gen. Tech. Rep. SO-44.
New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern
Forest Experiment Station. 132 pp.

Burnham, K. P., and D.R. Anderson. 2004. Multimodel inference: understanding
AIC and BIC in model selection. Sociological methods & research 33:261-304.

Campos-Cerqueira, M., W.J. Arendt, J.M. Wunderle, Jr., and T.M. Aide. 2017.
Have bird distributions shifted along an elevational gradient on a tropical
mountain? Ecology and Evolution, *7*:9914-9924.

Campos-Cerqueira, M., and T.M. Aide. 2021. Impacts of a drought and hurricane on tropical bird and frog distributions. Ecosphere 12:e03352. 10.1002/ecs2.3352

Charter, R.A. 1997. Confidence interval procedures for retest, alternate-form, validity, and alpha coefficients. Perceptual and Motor Skills 84:1488-1490.

Ewel, J.J., and J.L. Whitmore. 1973. The ecological life zones of Puerto Rico and the US Virgin Islands. USDA Forest Service, Institute of Tropical Forestry, Research Paper ITF-018.

Feng, Y., R.I., Negrón-Juárez, and J.Q. Chambers. 2020. Remote sensing and statistical analysis of the effects of hurricane María on the forests of Puerto Rico. Remote Sensing of Environment 247:111940.

Fiske, I., and R. Chandler. 2011. Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of statistical software 43:1-23.

Fuller, A.K., D.W. Linden, and J.A. Royle. 2016. Management decision making for fisher populations informed by occupancy modeling. The Journal of Wildlife Management 80:794-802.

Garcia-Rivera, J.E., A.P. Marrero, and W.M. Latalladi. 2018. General Surgery Residency Program Response Plan to Hurricane Maria in Puerto Rico. Journal of the American College of Surgeons 227:S219.

Gesch, D.B., and D. Maune. 2007. Digital elevation model technologies and
applications: the DEM user's manual. In American Society for Photogrammetry
and Remote Sensing 2:99-118.

Gould, W.A., C. Alarcón, B. Fevold, M.E. Jiménez, S. Martinuzzi, G. Potts, ... and
E. Ventosa. 2008. The Puerto Rico Gap Analysis Project volume 1: land cover,
vertebrate species distributions, and land stewardship. Gen. Tech. Rep. IITF-
39, 1.

Harris, N.L., A.E. Lugo, S. Brown, and T. Heartsill-Scalley. Luquillo Experimental
Forest: Research History and Opportunities. Experimental Forest and Range
EFR-1. Washington, DC: USDA Forest Service.

Herartsill-Scalley, T. 2012. Vegetation. *In* N.L. Harris, A.E. Lugo, S. Brown, and
T. Heartsill-Scalley. Luquillo Experimental Forest: Research History and
Opportunities. Experimental Forest and Range EFR-1. Washington, DC:
USDA Forest Service. 64-72.

Hu, T., and R.B. Smith. 2018. The impact of Hurricane Maria on the vegetation of
Dominica and Puerto Rico using multispectral remote sensing. Remote
Sensing 10:827-847. doi:10.3390/rs10060827

Hutto, R.L., S.M. Pletschet, and P. Hendricks. 1986. A fixed-radius point count
method for nonbreeding and breeding season use. Auk 103:593–602.

IUCN. 2004. IUCN Red List of Threatened Species. IUCN, Gland, Switzerland.
Available online at http://www.redlist.org.

Karanth, K.U., A.M. Gopalaswamy, N.S. Kumar, S. Vaidyanathan, J.D. Nichols, and D.I. MacKenzie. 2011. Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. Journal of Applied Ecology 48:1048-1056.

Kéry, M., and J.A. Royle. 2015. Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS. Academic Press, 789 pp.

Lloyd, J.D., C.C. Rimmer, and J.A. Salguero-Faría. 2019. Short-term effects of hurricanes Maria and Irma on forest birds of Puerto Rico. PLoS ONE 14:e0214432. DOI:10.1371/journal.pone.0214432.

Lugo, A.E. 1994. Preservation of primary forests in the Luquillo Mountains, Puerto Rico. Conservation Biology 8:1122-1131.

Lynch, J.F. 1991. Effects of Hurricane Gilbert on birds in a dry tropical forest in the Yucatan Peninsula. Biotropica 23:488–496.

MacKenzie, D.I., J.D. Nichols, G.B. Lachman, S. Droege, J.A. Royle, and C.A. Langtimm, 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.

Mazerolle, M.J. 2020. Model selection and multimodel inference using the AICcmodavg package. R package version ≥3.2.0. Available online at http://CRAN.R-project.org/package=AICcmodavg.

Morin, D.J., C.B. Yackulic, J.E. Diffendorfer, D.B. Lesmeister, C.K. Nielsen, Reid J., and E.M. Schauber. 2020. Is your ad hoc model selection strategy affecting your multimodel inference? Ecosphere, 11:e02997.

Nareff, G.E., P.B. Wood, D.J. Brown, T. Fearer, J.L. Larkin, and W.M. Ford. 2019. Cerulean Warbler (*Setophaga cerulea*) response to operational silviculture in the central Appalachian region. Forest Ecology and Management 448:409-423.

Odum, H.T., and R.F. Pigeon. 1970. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. Division of Technical Information, US Atomic Energy Commission.

Pagán, M. 1995. Habitat relationships of avian communities on an elevational gradient in the Luquillo Experimental Forest of Puerto Rico. M.S. Thesis. University of Puerto Rico, Río Piedras, USA, 99.

R Development Core Team. 2021. R: A language and environment for statistical computing. Available online at http://www.R-project.org. R Foundation for Statistical Computing, Vienna, Austria.

Rittenhouse, C.D., A.M. Pidgeon, T.P. Albright, P.D. Culbert, M.K. Clayton, C.H. Flather, and V.C. Radeloff. 2010. Avifauna response to hurricanes: Regional changes in community similarity. Global Change Biology 16:905–917.

Rivera-Milán, F.F., G.S. Boomer, and A.J. Martínez. 2014. Monitoring and modeling of population dynamics for the harvest management of scaly-naped pigeons in Puerto Rico. Journal of Wildlife Management 78:513-521.

Rollé, F.J. 1965. An observation of heavy predation by pearly-eyed thrasher. Wilson Bulletin. 77:296-297.

Royle, J.A. 2004. N-mixture models for estimating population size from spatially
    replicated counts. Biometrics 60:108-115.

Scatena, F.N. 1995. An assessment of climate change in the Luquillo Mountains
    of Puerto Rico. Pages 103-111. Geophysial Monogramph Series 89. American
    Geophysical Union, Wahsington, D. C. USA.

Silver, W.L., A.E. Lugo, and M. Keller. 1999. Soil oxygen availability and
    biogeochemistry along rainfall and topographic gradients in upland wet tropical
    forest soils. Biogeochemistry 44:301-328.

Snyder, N.F.R., J.W. Wiley, and C.B. Kepler. 1987. The Parrots of Luquillo:
    Natural History and Conservation of the Puerto Rican Parrot. Los Angeles, CA:
    Western Foundation of Vertebrate Zoology. 384 pp.

Tejeda-Cruz, C., and W.J. Sutherland. 2005. Cloud Forest bird responses to
    unusually severe storm damage. Biotropica 37:88–95.

Thomas, L., S.T. Buckland, E.A. Rexstad, J.L. Laake, S. Strindberg, S.L. Hedley,
    ... and K.P. Burnham. 2010. Distance software: design and analysis of
    distance sampling surveys for estimating population size. Journal of Applied
    Ecology 47:5-14.

Uriarte, M., J. Thompson, and J. K. Zimmerman. 2019. Hurricane María tripled
    stem breaks and doubled tree mortality relative to other major storms. Nature
    communications 10:1362-1369.

US Fish and Wildlife Service. 1999. Technical/Agency Draft Revised Recovery

    Plan for the Puerto Rican Parrot (*Amazona vittata*). USFWS Region 4, Atlanta,

    USA.

Van Belle, G. Statistical Rules of Thumb, 2002. Willey. Available online:

    https://www. wiley. com/en-us/Statistical+ Rules+ of+ Thumb% 2C+ 2nd+

    Edition-p-9780470144480 (accessed on 26 February 2021).

Wadsworth, F.H. 1951. Forest management in the Luquillo Mountains. I. The

    setting. Caribbean Forester 12:93-114.

Waide, R.B. 1991. The effect of Hurricane Hugo on bird populations in the

    Luquillo experimental forest, Puerto Rico. Biotropica 23:475-480.

Walker, L.R., D.J. Lodge, and R.B. Waide. 1991. An introduction to hurricanes in

    the Caribbean. Biotropic 23:313-316.

Walker, L. R., J. K. Zimmerman, D. J. Lodge, and S. Guzmán-Grajales. 1996. An

    altitudinal comparison of growth and species composition in hurricane-

    damaged forests in Puerto Rico. Journal of Ecology 84:877-889.

Weaver, P.L. 1990. Succession in the elfin woodland of the Luquillo Mountains of

    Puerto Rico. Biotropica 22:83-89.

Weaver, P.L., and W.A. Gould. 2013. Forest vegetation along environmental

    gradients in northeastern Puerto Rico. Ecological Bulletins 54:43-66.

Webster, P.J., G.J. Holland, J.A. Curry, and H.R. Chang. 2005. Changes in
    tropical cyclone number, duration, and intensity in a warming
    environment. Science 309:1844-1846.

White, T.H., J.A. Collazo, S.J. Dinsmore, and I. Llerandi-Román. 2014. Niche
    restriction and conservatism in a neotropical psittacine: the case of the Puerto
    Rican Parrot. *In* B. Devore, Ed. Habitat loss: Causes, Impacts on Biodiversity
    and Reduction Strategies. Nova Science Publishers, New York, NY. 83pp.

Wiley, J.W., and J. M. Wunderle Jr. 1993. The effects of hurricanes on birds, with
    special reference to Caribbean islands. Bird Conservation International 3:319-
    349.

Wunderle Jr., J.M. 1995. Responses of bird populations in a Puerto Rican forest
    to Hurricane Hugo: the first 18 months. Condor 97:879-896.

Wunderle Jr., J.M. 1999. Pre-and post-hurricane fruit availability: Implications for
    Puerto Rican parrots in the Luquillo Mountains. Caribbean Journal of Science
    35:249-264.

Wunderle Jr., J.M., D.J. Lodge, and R.B. Waide. 1992. Short-term effects of
    Hurricane Gilbert on terrestrial bird populations on Jamaica. The Auk,
    109:148–166.

Zimmerman, J.K., M.R. Willig, L.R. Walker, and W.L. Silver. 1996. Introduction:
    disturbance and Caribbean ecosystems. Biotropica 28:414-423.

Figures

Figure 1.1

Map of the Luquillo Experimental Forest and its location in NE Puerto Rico (grey area in the inserted map). Circles represent all sites sample. Different grey scale colors represents differences in elevation (m a.s.l.)
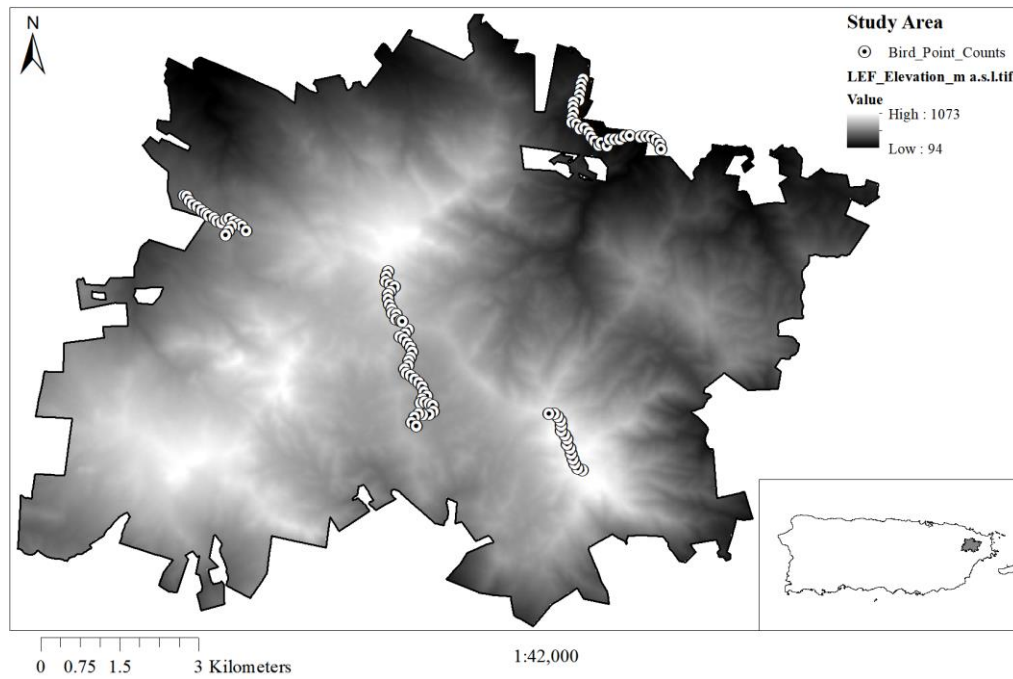
Figure 2.1

Pearly-eyed Thrasher modeled occupancy probability (A) and abundance (B) in 1998 (80-points), 2005 (110-points), and 2018 (110-points) in the Luquillo Experimental Forest, Puerto Rico. Bars represent 95% confidence intervals.
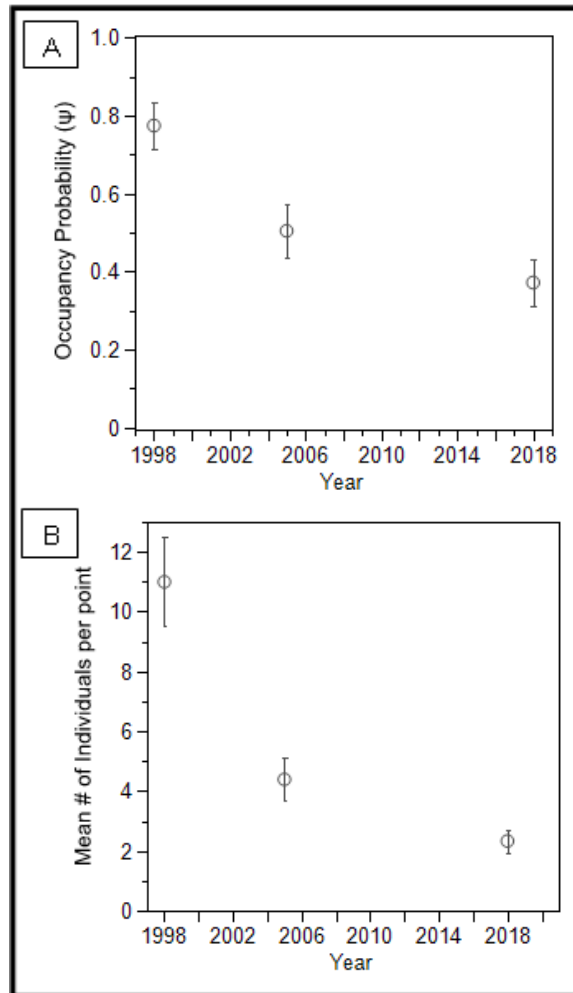
Figure 3.1

Pearly-eyed Thrasher mean modeled occupancy probability (A) and abundances
(B) along an elevation gradient in 1998 (orange - n = 80-points), 2005 (pink - n =
110-points), and 2018 (blue - n = 110-points) in the Luquillo Experimental Forest,
Puerto Rico.
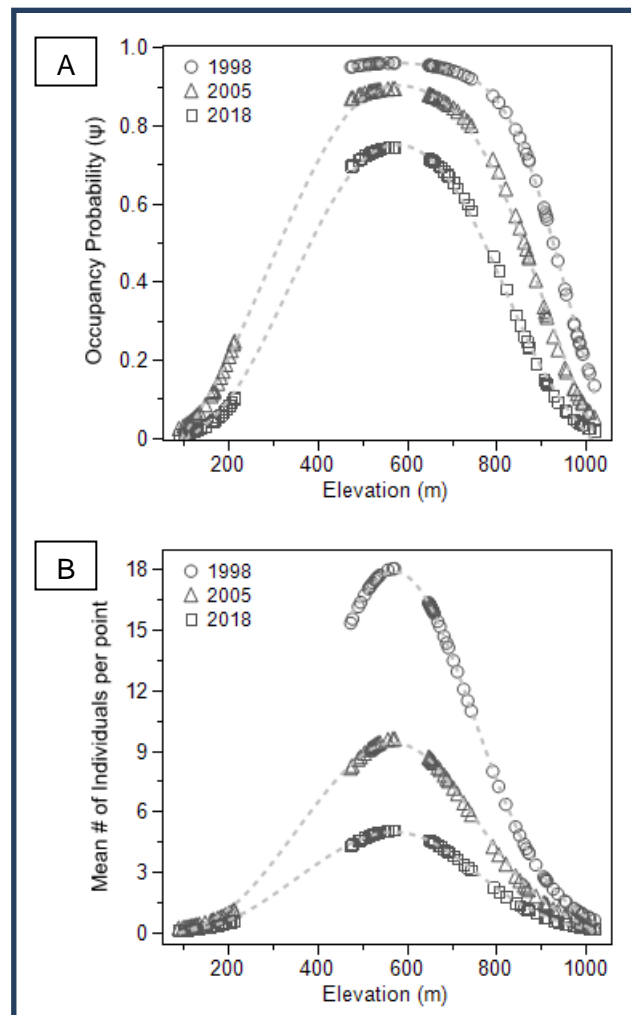
Table S1.1

Model selection results of detection probability sub-models with a single-season
occupancy model and a single-season n-mixture model analysis. Model selection
based on Akaike's Information Criterion (AICc), number of parameters (K), the
difference in AICc from the best fit model (ΔQAICc), model weight (AICc.Wt).
AICc is the Akaike's Information Criterion value for small sample sizes, which
measures the fit of a model relative to other models. Quasi- Akaike's Information
Criterion (QAICc) was used when there was an overdispersion in the global
model.

Occupancy Models	K	QAICc	ΔQAICc	QAICc.Wt
p (year + date)	5	278.8	0	0.84
p (year)	4	283.99	5.18	0.06
p (year + hurricanes)	5	284.54	5.73	0.05
p (year + time)	5	284.73	5.93	0.04
p (hurricane)	4	294.91	16.11	0
p (date)	4	296.98	18.18	0
p (.)	3	301.87	23.07	0
p (time)	4	302.64	23.84	0

N-Mixture Models	K	AICc	ΔAICc	AICc.Wt
p (year + date)	4	1435.2	0	1
p (year + hurricanes)	4	1457.27	22.07	0

p (year + time)	4	1463.3	28.1	0
p (year)	3	1467.59	32.39	0
p (hurricane)	3	1570.54	135.34	0
p (date)	3	1582.99	147.79	0
p (time)	3	1611.16	175.96	0
p (.)	2	1618.87	183.67	0

Table S2.1

Mean predicted estimate values of detection probability (P) across the years and visits. Included are the standard error (SE) and the 95% confidence intervals (Lower and Upper).

Year	Visits	P	SE	Lower	Upper
1998	1	0.70	0.01	0.68	0.73
	2	0.48	0.01	0.46	0.51
	3	0.27	0.01	0.25	0.29
2005	1	0.70	0.01	0.68	0.72
	2	0.48	0.01	0.45	0.50
	3	0.28	0.01	0.27	0.30
2018	1	0.55	0.01	0.53	0.58
	2	0.44	0.02	0.41	0.47
	3	0.27	0.01	0.25	0.29

Table S3.1

Model selection result of occupancy probability (Ψ). Covariates considered were elevation, forest type (Tabonuco, Palo Colorado, Sierra Palm, and Elfin Forest), hurricane damage, and years. Included are the linear and quadratic term for elevation and forest type. Model selection based on Quasi-Akaike's Information Criterion (QAICc), number of parameters (K), the difference in QAICc from the best fit model (ΔAICc), model weight (QAICc Wt.). AICc is the Akaike's Information Criterion value for small sample sizes, which measures the fit of a model relative to other models. Models for detection (p) were fixed without covariables (.). We assumed constant detection (p[.]) and did not include detection covariates in occupancy models.

Models	K	QAICc	ΔQAICc	QAICc.Wt
ψ (year + elevation^2)	5	256.22	0	1
ψ (elevation^2)	4	269.04	12.81	0
ψ (year + elfin)	5	274.31	18.09	0
ψ (year + palo colorado)	5	276.53	20.31	0
ψ (year + palo colorado^2)	5	278.94	22.72	0
ψ (year + enfin^2)	5	279.12	22.9	0
ψ (year + hurricane)	5	283.56	27.34	0
ψ (year + tabonuco)	5	285.76	29.54	0
ψ (year)	4	286.06	29.83	0
ψ (year + sierra palm)	5	286.95	30.73	0

ψ (year + tabonuco^2)	5	287.17	30.95	0
ψ (year + sierra palm^2)	5	287.75	31.53	0
ψ (year + elevation)	5	288.04	31.82	0
ψ (palo colorado)	4	291.42	35.2	0
ψ (elfin)	4	294.06	37.84	0
ψ (palo colorado^2)	4	295.58	39.36	0
ψ (elfin^2)	4	297.26	41.04	0
ψ (tabonuco)	4	300.08	43.86	0
ψ (hurricane)	4	300.41	44.18	0
ψ (.)	3	301.87	45.65	0
ψ (tabonuco^2)	4	302.04	45.82	0
ψ (sierra palm)	4	302.16	45.94	0
ψ (elevation)	4	302.83	46.6	0
ψ (sierra palm)	4	303.42	47.2	0

Table S4.1

Mean predicted estimate values of occupancy probability (Ψ) across the years. Included are the standard error (SE) and the 95% confidence intervals (Lower and Upper).

Years	Estimates	SE	Lower	Upper
1998	0.95	0.01	0.94	0.96
2005	0.87	0.01	0.86	0.88
2018	0.70	0.01	0.69	0.72

Table S5.1

Model selection result for thrasher abundance (λ). Covariates considered were elevation, forest type (tabonuco, palo colorado, sierra palm, and elfin forest), hurricane damage, and years. Also included are the linear and quadratic terms for elevation and forest type. Model selection was based on Akaike's Information Criterion (AICc), number of parameters (K), the difference in AICc from the best fit model (ΔQAICc), model weight (AICc.Wt). AICc is the Akaike's Information Criterion value for small sample sizes, which measures the fit of a model relative to other models. Models for detection (p) were fixed without covariables (.). We assumed constant detection (p[.]) and did not include detection covariates in abundance models.

Models	K	AICc	ΔAICc	AICc.Wt
λ (year + elevation^2)	4	1252.14	0	1
λ (year + elfin)	4	1349.86	97.72	0
λ (elevation^2)	3	1388.64	136.5	0
λ (year + elfin^2)	4	1394.85	142.71	0
λ (year + palo colorado)	4	1395.62	143.48	0
λ (year + palo colorado^2)	4	1421.37	169.23	0
λ (year + tabonuco)	4	1447.71	195.57	0
λ (year + hurricane)	4	1449.67	197.53	0
λ (year + sierra palm)	4	1456.02	203.88	0

λ (year + tabonuco^2)	4	1457.43	205.29	0
λ (year + elevation)	4	1457.78	205.65	0
λ (year)	3	1458.46	206.33	0
λ (year + sierra palm^2)	4	1459.96	207.82	0
λ (palo colorado)	3	1536.69	284.55	0
λ (elfin)	3	1541.95	289.81	0
λ (elfin^2)	3	1572.23	320.09	0
λ (palo colorado^2)	3	1575.55	323.41	0
λ (hurricane)	3	1579.12	326.98	0
λ (tabonuco)	3	1587.3	335.16	0
λ (tabonuco^2)	3	1608.19	356.06	0
λ (sierr palm)	3	1609.52	357.39	0
λ (elevation)	3	1616.98	364.85	0
λ (.)	2	1618.87	366.73	0
λ (sierra palm^2)	3	1618.9	366.77	0

Table S6.1 Mean predicted estimate values of abundance (λ) across the years. Included are the standard error (SE) and the 95% confidence intervals (Lower and Upper).

Years	Estimates	SE	Lower	Upper
1998	15.83	0.27	15.30	16.37
2005	8.40	0.13	8.15	8.66
2018	4.46	0.08	4.31	4.61

Chapter 2: Short-term Response of Pearly-eyed Thrashers to Post-Hurricane Habitat Changes in the Luquillo Experimental Forest, Puerto Rico.

Alberto C. Cruz-Mendoza[a], Laura L. Fidalgo-De Souza[a], Frank F. Rivera-Milán[b], Jessica Ilse[c], Jazlynn Hall[c] & Joseph M. Wunderle, Jr.[a, d]

[a] Department of Environmental Science, University of Puerto Rico, Rio Piedras, PR 00931

[b] Division of Migratory Bird Management, Branch of Assessment and Decision Support, United States Fish and Wildlife Service, 11510 American Holly Drive, Maryland 20708, USA

[c] Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, NY, USA.

[d] International Institute of Tropical Forestry, USDA Forest Service, Sabana Field Research Station, HC 02 Box 6205, Luquillo, Puerto Rico 00773, USA

Abstract

After hurricanes, birds may shift sites in response to vegetation damage or changes in resource availability. Pearly-eyed Thrashers (*Margarops fuscatus*; thrasher hereafter) have been observed to increase abundance in damaged sites after hurricanes and therefore we expected thrasher site occupancy and abundance to increase in the most damaged sites. We tested this hypothesis by surveying 158 points along an elevation gradient in the Luquillo Mountains in the year (2018) following Hurricane María (2017). Thrasher occupancy was estimated with a single-season model and abundance was estimated with an *N*-mixture model. Sierra palm cover and the interaction between NDVI and elevation were the most important covariates for occupancy and abundance estimates. The relationships between sierra palm cover with thrashers occupancy and abundance were positive and consistent with the importance of sierra palm fruit in the thrasher diet. The NDVI per site showed a negative linear relationship with elevation corroborating previous findings that vegetation damage was greatest at high elevations. Thrasher occupancy and abundance increased with elevation only in sites with minimal or no damage (NDVI > 0.4). Above mid elevation (> 600 m), thrashers occupancy and abundance decreased with elevation in damaged sites (NDVI < 0.4). In contrast to our predictions, thrashers at higher elevations (> 600 m) had a higher probability of occupying sites with minimal or no storm damage than damaged sites where fruit was likely scarce in the first year after Hurricane María. Thrashers may delay colonization

of damaged sites at high elevation because of the slow plant regrowth there which retards fruiting.

Introduction

Natural disturbances have the potential to influence ecosystems, community dynamics and biological cycles in different ways (Pickett et al. 1989). Disturbances such as hurricanes, droughts, and sea level rise are predicted to increase in frequency and/or intensity due to global climate change (Webster et al. 2005, Knutson et al. 2010, IPCC 2014). Hurricane-induced environmental changes may influence population processes and affect population densities (Ricklefs 2000). In some regions, such as the Caribbean, hurricanes occur with sufficient frequency to influence the structure and species composition of biotic communities (Odum and Pigeon 1970, Walker et al. 1991). Hurricanes may alter forest structure and composition by defoliation, breakage of tree limbs and trunks, and uprooting of trees (Walker 1991a,b). For birds, hurricane-induced changes in forest structure and productivity can influence availability of foraging substrates, food supplies, nest or roost sites, predation vulnerability, and change microclimates (Wiley and Wunderle 1993). Responses of birds to these hurricane effects may be species-specific (Rittenhouse 2010) and some species may benefit from these disturbances (Greenberg and Lanham 2001, Tejeda-Cruz and Sutherland 2005).

Little is known about the relationship between post-hurricane bird population changes in association with severity of hurricane damage to vegetation (Wiley and Wunderle 1993, Brown et al. 2011). In storm-damaged sites, avian food resources such as fruits, seeds, and nectar may be sparse or absent in the immediate storm aftermath (Wunderle 1999) contributing to

declines in nectarivores and frugivore/seedeaters in these sites (Wunderle et al. 1992, Llyod et al. 2019). Conversely in defoliated sites, potential prey such as frogs, lizards, and insects may be more exposed and vulnerable to predators (Wiley and Wunderle 1993). Canopy loss may cause canopy dwelling *Anolis* lizards to concentrate in high densities in the fallen canopy debris on the ground where they may be more vulnerable to predators (Reagan 1991). However, with time and increased light exposure in damaged sites, new leaf production may result in herbivorous insect outbreaks (Torres 1992). Additionally, increased primary productivity (Wang and Hall 2004) may contribute to bursts of flowering and fruiting in understory plants after canopy cover has been reduced (Wunderle et al. 1992, Wunderle 1995, Angulo Sandoval et al. 2004). Therefore, the time after storm impact may be an important factor influencing avian habitat suitability of hurricane-damaged sites.

Hurricane-damaged sites may provide opportunities for colonization by Pearly-eyed Thrashers (*Margarops fuscatus*; thrashers hereafter) a species which may colonize vacant niches in disturbed habitats in the Caribbean (Arendt 2006). Colonization of vacant niches is facilitated by the thrasher's high dispersal ability, aggressive behavior, and opportunistic diet, all of which led Arendt to designate the thrasher as a "supertramp". Observations of thrasher use of heavily damaged sites shortly after hurricanes in the Luquillo Experimental Forest (LEF hereafter) in Puerto Rico suggested to Arendt (2006) that thrashers colonized niches or sites abandoned by other species. Shortly after a hurricane (< 3 months) thrashers may shift from canopy to ground level following canopy

loss as found in lowland forest of the LEF (Waide 1991, Wunderle 1995). A shift of longer duration was documented for thrashers after Hurricane Maria struck St. John in the U.S. Virgin Islands. Here, two years after Hurricane María, thrasher abundance decreased in upland moist forest and increased in lowland dry woodlands (Askins and Ewert 2020). Site shifts were also indicated for thrashers shortly (< 1 yr) after Hurricane María when probability of site occupancy increased from pre-hurricane levels in the Cordillera Central of Puerto Rico (Llyod et al. 2019). These post-hurricane shifts in site occupancy may occur along more extensive elevation gradients as found for thrashers and other species in the LEF (Campos-Cerqueira and Aide 2021) and elsewhere (Wiley and Wunderle 1993).

An opportunity to quantify thrashers response to variation in storm damage was provided by the 2017 hurricanes Irma and Maria, which caused substantial vegetation damage in the LEF (Uriarte et al 2019, Feng et al. 2020, Hall et al. 2020). Hurricane Irma, passed ~80 km northeast of Puerto Rico on 6 September as a Category 5 (Saffir-Simpson scale) hurricane with wind speeds approaching 300 km/h. Fourteen days later, on 20 September, Hurricane Maria made landfall on southeastern Puerto Rico and crossed diagonally over the island exiting on the northwest coast as a Category 4 storm with maximum sustained winds of ~250 km/h. Hurricane Maria was the most intense hurricane recorded in Puerto Rico for almost ninety years, after Category-5 Hurricane San Felipe II in 1928 (Garcia-Rivera et al. 2018). The severity of hurricane damage to vegetation varied with local and landscape-scale factors (Hall et al. 2020),

including an increase in damage severity with elevation (Hu and Smith 2018, Feng et al. 2020). This led us to predict that thrasher site occupancy and abundance would be highest in the most severely damaged sites at high elevations in the LEF during the first year (2018) after the hurricanes.

Methods

Field-site Description

The study was conducted in the Luquillo Experimental Forest (also known as the El Yunque National Forest, henceforth LEF) in northeastern Puerto Rico (Fig. 1.2). The LEF is the largest protected area (115 km²) with primary forest on the island (Lugo 1994). The forest has a long history of ecological research (Harris et al. 2012) including studies on disturbances, especially the effects of hurricanes on forest ecosystems (Brokaw et al. 2012, Zimmerman et al. 2020). The LEF includes most of the Luquillo Mountains which have a maximum elevation of 1074 m a.s.l. and have a strong effect on abiotic factors (temperature, rain, humidity), and the biota (Weaver and Gould 2013). The temperature differs by 7°C for mean maximum values between low and high sites, but annually varies little with elevation for mean monthly temperatures (3-3.5 °C). Annual rainfall ranges from an average of 2450 mm/yr in the lowlands to 4000 mm/yr at higher elevations. The LEF has five ecological life zones: subtropical moist forest, subtropical wet forest, subtropical rainforest, lower montane wet forest, and lower montane rain forest (Ewel and Whitmore 1973), as well as four major forest types (Wadsworth 1951). The main forest types includes: (1) the tabonuco forest which is dominated by *Dacryodes excelsa* V. (Candlewood or Tabonuco) and occurs between 150 and 600 m, most commonly in the subtropical moist and wet forests; (2) the palo colorado forest which is dominated by *Cyrilla racemiflora* L. (Swamp titi or Palo Colorado) and occurs between 600 and 950 m, most commonly in the lower montane wet and rainforests; (3) the elfin forest which is

64

dominated by *Tabebuia rigida* Urb. (Roble de Sierra) and *Eugenia borinquensis*

B. (Guayabota de Sierra), occurring above 950 m and most commonly in the

lower montane rain forest; and (4) the sierra palm forest which is dominated by

Prestoea acuminata var. montana G. (Sierra Palm or Palma de Sierra) and

occurs anywhere interspersed between the elfin and palo colorado forests. The

sierra palm forest is mostly found on steep slopes at higher elevations.

Data Collection

During April-August 2018, we sampled 158 georeferenced points, which were

visited three times each to sample birds. All points were surveyed during April-

May in the first visit, late June-early July in the second visit, and late July-early

August in the third visit. Surveys were conducted by teams of two observers

situated at each point for 10 minutes, with one observer recording the data and

the other measuring detection distances (Burnham et al. 2004, Rivera-Milan et al.

2014). Distances to single thrashers or clusters were measured with a laser

rangefinder (Rivera-Millan et al. 2014). We defined a cluster as two or more birds

within 10 m of each other, showing similar behavior. When vocalizing birds could

not be visually detected, we measured distances to the nearest horizontal

location and grouped detections using the following distance categories: 0–5, 6–

15, 16–25, 26–50, 51–75, 75–100, and 100 < m. Based on the distances

measured, we truncated the count data at 50 m and define an area of 0.79 ha

(~0.01 km^2) for occupancy and abundance estimations. All teams were trained in visual and audio identification of thrashers to minimize species misidentifications.

Forest Covariates

We characterized forest structure at each point using photographic (image-based) descriptors of habitat geometry to relate bird species presence to habitat structure (Martin and Proulx 2016), around each point center. We took photographs using an EOS Digital Rebel$^©$ camera. Photos were taken in the four cardinal directions, both horizontal (0°) and at a 45° angle (Fig. S1.2; see Table S1.2 for camera settings). The eight photos per point were taken three times for a total of 24 images per point. The photos were taken with a camera mounted on tripod at one meter above the ground. At 0° we calculated the mean information gain (MIG, Proulx and Parrott 2008) and the greenness index (ExG – ExR, Meyer and Camargo Neto 2008), and at 45° we calculated the indirect leaf area index (LAI, Macfarlane 2011) using R Image Analysis Primer package (Martin 2015). The MIG index is a good predictor of forest structure complexity (Proulx and Parrot 2008, 2009) and the ExG – ExR is a good predictor of the interior forest biomass. MIG and ExG – ExR values were processed for all 12 images at 0° per point. As Proulx and Parrott (2008) suggest, we calculated the mean for the 12 images at zero degrees at each point. The LAI is defined as the area of foliage (one surface only) per unit ground area (Chen and Black 1992). This index is an important quantity controlling for the physical and biological processes of plant canopies (Chen and Black 1992). As with the 0° images, LAI values were processed for all 12 images at 45°, for which we calculated the mean for the 12

images per point. All image-based measurements were taken from January to April 2019, approximately sixteen months after Hurricane María.

In addition to the image-based method, we also used spatial analysis to obtain other forest covariates from satellite imagery (Landsat 7.8) and several available GIS layers. We calculated the normalized difference vegetation index (NDVI) from the Landsat 7.8 images that had a resolution of 30 meters square per pixel, to measure the hurricane damage. NDVI is derived from reflectance values that are calculated separately in two wavelength bands in the visible (0.5-0.7 μm) and near infrared (0.7-0.9 μm) regions of the spectrum (Carlson and Ripley 1997). NDVI values range from -1.0 to 1.0, with high values associated with high levels of vegetation cover. As a measure of vegetation cover, NDVI has been used to quantify vegetation productivity and health (Wallis et al. 2016). The NDVI data were obtained from stack image layers where the mean of NDVI values from March to September 2018 were calculated. The values represent an average of 9 pixels (i.e., a center pixel over the point count site and eight surrounding pixels), comprising an area of 90 X 90 meters. This method was used to avoid NDVI values of zero associated with roads and buildings. For this research, we assume that low values of NDVI were from points with high hurricane damage and high values of NDVI were from sites with low hurricane damage (Rodgers et al. 2009). This is a reasonable assumption because reduced vegetation cover is typical of hurricane damage (Lugo 2008). For example, Rodgers et al. (2009) found that the low NDVI values obtained in the immediate aftermath of Hurricane Katrina were similar to the low NDVI values

67

obtained ~8 months post-hurricane; however, pre- versus post-hurricane NDVI

values declined by an average of 49%. Other GIS layers were used to quantify

landscape traits including slope, aspect, elevation, distance to road, and forest

type. For slope, aspect, and elevation we used the density elevation model

(DEM, Gesch and Maune 2007). Forest type was obtained from the GIS layer

from the Puerto Rico GAP analysis (Gould et al. 2008). The forest types were

divided in to four principal forests: tabonuco, palo colorado, sierra palm, and elfin,

as described previously. Additionally, we used the change in canopy height

obtained by Lidar (data from Hall et al. 2020).

Occupancy and Abundance modelling

We used single-season occupancy models (MacKenzie et al. 2002) to

estimate detection probability (p) and occupancy (ψ) and to explore the influence

of survey-specific and site-specific covariates in 2018. Additionally, we used N-

mixture models (Royle 2004) to estimate detection and abundance (lambda [λ]

per survey point and across survey points). This method assumes constant

occupancy and abundance or population closure to births, deaths, immigration,

or emigration between survey occasions during April-August 2018. Thus, we

fitted and compared occupancy and N-mixture models that combined data from

the point-count surveys of 2018. The detection model included covariates of

NDVI, ordinal date of the survey (dates), start time of the survey (time), wind

speed of the survey (wind), and precipitation (prec). Because of the high number

of covariates for abundance and occupancy sub-models, we examined a

pairwise correlation for all covariates to ensure we did not have multicollinearity issues (Table S2.2). After the covariate selection, we modeled abundance and occupancy as a function of the NDVI, MIG, LAI, ExG – ExR, slope, aspect, sierra palm, and elevation. All numeric covariates were re-scaled to a mean and standard deviation (SD) of 0 and 1 respectively.

Model Selection

We used a multi-stage model fitting approach for many potential models (Karanth et al. 2011, Fuller et al. 2016, Nareff et al. 2019). We used a secondary candidate set strategy that fit sub-models independently and combined the top set of models from each sub-model for selection in the final stage (Bromaghin et al. 2013, Morin et al. 2020). We used R package 'UNMARKED' (Fiske and Chandler 2011) in R version 4.0.5 (R Core Team 2021) for model fitting. We initially used a forward stepwise selection process to identify the importance of the five covariates for detection probability in both models (Table S3.2 and S4.2). Next, for occupancy and abundance, we used the eight covariates, previously mentioned, to do the same analyses as in the first step for detection (Table 1.2 and 2.2). We also considered interactions between NDVI and other covariates in individual models with biological relevance to our hypothesis. For each sub-model, we selected all estimated parameters that had significant importance ($p < 0.05$, see Tables S5.2 and S6.2). Finally, in both model selection processes, we used all covariates selected for each sub-model in the two previous steps to run a backward stepwise selection model. We calculated the effective sample sizes

(n-*ess*) to obtain the corrected Akaike's Information Criterion (AICc). We selected

the most parsimonious model with a difference between models in AICc values

less than or equal to two (ΔAICc ≤ 2). Finally, we plotted the predicted parameter

values of post-hurricane thrasher occupancy and abundance for supported

model covariates to examine the relationship between them. Results are

presented as means with standard errors (SEs) and 95% confidence intervals

(CI), using the predicted values for each point and the two-tailed z score to

estimate them (Charter 1997). We determined statistical difference by the

absence of overlap in the 95% CI, but we consider that a < 30% of overlap in the

CIs are still significantly different (Van Belle 2002).

Results

We detected 47 thrashers at 28 of 158-points during the 2018 surveys. The top detection sub-model included ordinal date and start time of the point counts (Table 1.2 and 2.2). The β estimates from the top models for both covariates showed negative effect on detection, but only ordinal date was significant ($p = 0.03$, see Table S7.2, for betas estimates). Although detection declined with ordinal dates, there were no significant differences in detection probability between individual visits, indicating constant detection (~ 11% detection probability) during the three visits of the study (see Table S8.2, for predicted detection estimates).

Model selection results for occupancy (e.g., Ψ = a + sierra palm 0.9 [0.4] + ndvi:elevation 1.1 [0.6]) and abundance (e.g., λ = a + sierra palm 0.4 [0.1] + ndvi:elevation 0.9 [0.4]), both indicated that the most supported model included the interaction between NDVI and elevation, and sierra palm cover (Table 1.2 and 2.2). The top model predicted a mean occupancy of 0.30 [0.12 SE], 95% CI = 0.12-0.57. For abundance, the top model predicted a mean site estimate of 0.96 [0.67 SE], 95% CI = 0.24-3.85. The relationships between sierra palm cover with occupancy and with abundance were both significantly positive (Fig. 2.2). In addition, the NDVI per site showed a negative linear relationship across the elevational gradient with high elevation sites showing more low values of NDVI (Fig. 3.2) As in the previous chapter, occupancy and abundance estimates were highest at mid elevation. However, occupancy and abundance values showed positive interactions of NDVI with elevation. This interaction indicated that

occupancy and abundance increased with elevation at sites with little or no

vegetation damage (NDVI > 0.40). Correspondingly, in heavily damaged sites,

thrasher occupancy and abundance displayed negative relationships with

elevation (Fig. 4.2). However, sites with high vegetation damage (NDVI $\leq$ 0.40)

were found only above 600 m asl or mid elevation (Fig. 4.2).

Discussion

Pearly-eyed Thrasher detection probability declined across the three survey visits, although no significant differences were found in detectability between the three visits in pair-wise comparisons. The overall decline in detectability was consistent with expectations that thrashers would be easier to detect during their normal breeding season (January to July), when they are most vocal (Arendt 2006). However, as found in the previous chapter, detectability probabilities in the first visit in 2018 were lower than detectability probabilities during the first visits in two pre-hurricane years (1998, 2005 – Cruz-Mendoza et al. in prep). As argued in the previous chapter, the lower post-hurricane detectability (i.e., lower vocalization rate) during visit one relative to pre-hurricane detectability probabilities during the corresponding months were consistent with a post-hurricane depression of normal thrasher breeding. Depressed and delayed thrasher breeding in the first nesting season after hurricanes was found by Arendt (2006) following both hurricanes Hugo and Georges. This depressed nesting activity after a hurricane has been attributed to the loss of sierra palm fruits (Wunderle 1999), which are important for thrasher reproduction (Arendt 2006, Beltrán et al. 2010). Also, the quality of sierra palm fruits may decline in the immediate aftermath of hurricanes (Thompson Baranello 2000). Therefore, a decline in fruit abundance and quality may have contributed to delayed thrasher reproduction in 2018, as also documented in Puerto Rican Parrot breeding after Hurricane Hugo (Wunderle 1999).

Consistent with the importance of sierra palms for thrashers were our findings of post-hurricane thrasher occupancy and abundance increases with the percentage of sierra palm forest cover at a site. This finding was not surprising given the importance of sierra palm fruit in the thrasher diet (Arendt 2006). Although palm fruits were generally scarce after Hurricane María in 2018, we did observe scattered patches of intact or lightly defoliated palms, which retained fruit (Cruz-Mendoza pers. obs.). The post-hurricane scarcity of fruit may have caused thrashers to wander more widely in search of the few remaining palm fruits thereby increasing thrasher home range sizes, as observed in parrots after Hurricane Georges (Collazo et al. 2003, White et al. 2005). Increased wandering or movement by thrashers could contribute to higher site occupancy and abundance in sites with abundant palm trees.

Hurricane damage to vegetation, as measured by NDVI, increased with elevation in the LEF (Fig. 3.2) and was consistent with previous findings (Hu and Smith 2018, Feng et al. 2020). Along this gradient, however, thrasher occupancy and abundance displayed a complex interaction with vegetation damage (i.e., NDVI) and elevation. Thrasher occupancy and abundance increased with elevation only in sites with slight or no defoliation (NDVI > 0.4) across the elevation gradient. Above mid elevation (> 600 m) however, thrasher occupancy and abundance decreased with elevation in damaged sites (NDVI < 0.4). Thus, in contrast to our predictions, thrashers at high elevations (> 600 m) occurred in sites with minimal or no storm damage and were mostly absent from nearby damaged sites where fruits were scarce. This post-hurricane shift in the first year

after Hurricane María from damaged to undamaged sites at high elevations may reflect a thrasher response to fruit scarcity in damaged sites, as observed in other bird species shortly after hurricanes (Waide 1991, Wunderle 1995).

Our incidental observations of vegetation damage caused by the two hurricanes were consistent with previous post-hurricane studies. For instance, shortly after Hurricane Hugo, Brokaw and Grear (1991) demonstrated that the average maximum canopy height decreased in sample plots in subtropical wet forest (tabonuco), lower montane wet forest (palo colorado) and in lower montane rainforest (cloud forest) in the LEF. Moreover, the extent of area covered with low canopy (height < 2 m) showed a 6- to 60-fold increase after Hugo, with low canopy areas mostly created on ridges. As Brokaw and Grear (1991) recognized, the decrease in canopy height and expansion of areas with low canopy may facilitate greater light penetration to the forest understory, thereby accelerating vegetation regeneration (e.g., You and Petty 1991) and promoting colonization and growth of pioneer trees (e.g., Walker 1991a, b). Although pioneer shrubs and trees which bear fruits consumed by thrashers (*Miconia spp., Cecropica schreberiana, Clusia gundlachii, and Clibadium erosum*; Arendt 2006) occur in these low canopy damaged sites at high elevations (Wunderle, unpubl. observations), fruits were scarce there in the first year (2018) following the hurricanes. This fruit scarcity in damaged sites at high elevation in addition to scarcity in damaged palm forest patches at high elevation probably contributed to the low thrasher site occupancy and abundance there in 2018.

By the second post-hurricane year (2019), the probability of thrasher occupancy at high elevations (> 600 m) increased above pre-hurricane (2015) values (Campos-Cerqueira and Aide 2021). We believe the 2019 increase in thrasher occupancy in high elevation sites coincided with increased fruit availability associated with a flush of fruiting in the damaged low canopy sites and in palm forests at high elevations. Supporting this contention was a post-hurricane fruit flush in the second year after Hurricane Hugo in several tree species, including sierra palms at sites from 450 to 730 m in the LEF (Wunderle 1999). Canopy loss and concomitant light exposure likely contributed to a fruit flush in the second year as demonstrated by an increase in fruit abundance with decreased percent canopy cover over understory sierra palms (Gregory and Sabat 1996).   Corresponding with the post-hurricane fruit flush may have been an increase in thrasher breeding effort as occurred in the second year after Hurricane Hugo (Arendt 2006).

Because of the destructive power of hurricanes Irma and Maria to the forest structure and composition (Uriarte et al. 2019, Feng et al. 2020, Hall et al. 2020), we expected that some vegetation structure covariate(s) would show a strong influence on thrasher site occupancy and abundance in the LEF. Unexpectedly, however, none of the forest structure covariates were included in the final model including MIG, LAI, ExG –ExR, and Δ canopy height. Also, absent from the final model were other landscape covariates such as aspect and slope, which are also known to be correlated with hurricane damage (Hall et al. 2020). Although the NDVI measurements were obtained during March to September

2018 and the photographic descriptors were taken later (January to April 2019) when vegetation recovery had likely advanced beyond the dates of the NDVI measures, correlations with NDVI were reasonably high for ExG-ExR (0.47) and LAI (0.48), but not MIG (0.12) (see Table S2.2).

Scale or size of the area sampled may have been an important factor in relation to the weak or non-existent correlations of topographic factors with vegetation damage measurements and with thrasher site occupancy and abundance. For example, the small size of sample plots (50 x 20 m) were attributed by Brokaw and Grear (1991) for their failure to find expected correlations between vegetation damage and aspect in the LEF. Similarly, in Jamaican forests, hurricane-damaged forest appeared to be correlated with aspect at the landscape scale, but not at a smaller local scale where aspect effects were less consistent (Bellingham 1991). Therefore, scale differences among our measured variables may have accounted for lack of correlation of NDVI with topographic variables or photographic measures of vegetation structure at point count sites. In addition, some damage or topographic variables measured at point count sites may have characterized only a small (and potentially non-representative) portion of the home range used by thrashers, especially if thrashers were wandering more widely after the hurricane.

In conclusion, the heavy reliance of Pearly-eyed Thrashers on sierra palm fruits for food may facilitate their persistence in the LEF. It appears the high thrasher occupancy and abundance at mid elevation is due to the mixed forest cover of palo colorado and sierra palm. Large diameter trees, frequent in the

palo colorado forest, provide cavities for thrasher nesting at mid to high elevations (Arendt 2004, 2006). The resistance (low mortality) and resilience (rapid recovery and fruiting) of sierra palms to hurricanes (Uriarte et al. 2019) and the thrasher omnivorous diet and its high reproductive rate may help thrashers to recover faster from hurricanes than most other bird species in the LEF. Although, contrary to expectations, we found that thrashers at high elevations displayed lower occupancy and abundance in damaged sites than in undamaged sites in the first year after Hurricane María. By the second year after María, however, thrasher occupancy at high elevation increased above baseline values (Campos-Cerqueira and Aide 2021), suggesting that thrashers colonized damaged sites once there was sufficient time for plant recovery and fruiting. This indicates that thrasher colonization of damaged sites after disturbance may be strongly influenced by the resilience of the vegetation and resources in the disturbed site.

Acknowledgments

Literature Cited

Angulo-Sandoval, P., H. Fernández-Marín, J.K. Zimmerman, and T.M. Alde. 2004. Changes in patterns of understory leaf phenology and herbivory following hurricane damage. Biotropica 36:60-67.

Arendt, W.J. 2004. Open- and cavity-nesting traits merge in the evolution of an avian supertramp, the pearly-eyed thrasher (*Margarops fuscatus*). Ornitologia Neotropical 15:455–465.

Arendt, W.J. 2006. Adaptations of an avian supertramp: distribution, ecology, and life history of the pearly-eyed thrasher (*Margarops fuscatus*). US Department of Agriculture, Forest Service, International Institute of Tropical Forestry, Gen. Tech. Rep. 27.

Askins, R.A., and D.N. Ewert. 2020. Resistance and resilience of Virgin Islands bird populations following severe hurricanes. Wilson Journal of Ornithology 132:898-910.

Bellingham, P.J. 1991. Landforms influence patterns of hurricane damage: evidence from Jamaican montane forests. Biotropica 23:427-433.

Beltrán, J.W., J.M. Wunderle Jr., and W.J. Arendt. 2010. Changes in home range of breeding and post-breeding male Pearly-eyed Thrashers in the Luquillo Mountains of Puerto Rico. Ornitologia Neotropical 21:409-423.

Brokaw, N.V.L., T. A. Crowl, A.E. Lugo, W. H. McDowell, F. N. Scatena, R. B. Waide, and M.R. Willig. 2012. A Caribbean Forest Tapestry: The

Multidimensional Nature of Disturbance and Response. Oxford University Press, New York.

Brokaw, N.V., and J.S. Grear. 1991. Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. Biotropica 23:386-392.

Bromaghin, J.F., T.L. McDonald, and S.C. Amstrup. 2013. Plausible combinations: An improved method to evaluate the covariate structure of Cormack-Jolly-Seber mark-recapture models. Open Journal of Ecology 3:11-22.

Brown, D.R., T.W. Sherry, and J. Harris. 2011. Hurricane Katrina impacts the breeding bird community in a bottomland hardwood forest of the Pearl River basin, Louisiana. Forest Ecology and Management 261:111-119.

Burnham, K.P., and D.R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological methods & research 33:261-304.

Campos-Cerqueira, M., W.J. Arendt, J.M. Wunderle Jr., and T.M. Aide. 2017. Have bird distributions shifted along an elevational gradient on a tropical mountain? Ecology and Evolution *7*:9914-9924. https://doi.org/10.1002/ece3.3520

Campos-Cerqueira, M., and T.M. Aide. 2021. Impacts of a drought and hurricane on tropical bird and frog distributions. Ecosphere 12(1): e03352. 10.1002/ecs2.3352

Carlson, T.N., and D.A. Ripley. 1997. On the relation between NDVI, fractional

vegetation cover, and leaf area index. Remote sensing of Environment 62:

241-252.

Charter, R.A. 1997. Confidence interval procedures for retest, alternate-form,

validity, and alpha coefficients. Perceptual and Motor Skills 84:1488-1490.

Chen, J. M., and T.A. Black. 1992. Defining leaf area index for non-flat

leaves. Plant, Cell & Environment 15:421-429.

Collazo, J.A., T.H. White Jr, F.J. Vilella, and S.A. Guerrero. 2003. Survival of

captive reared Hispaniolan parrots released in Parque Nacional del Este,

Dominican Republic. The Condor 105:198-207.

Ewel, J.J., and J.L. Whitmore. 1973. The ecological life zones of Puerto Rico and

the US Virgin Islands. USDA Forest Service, Institute of Tropical Forestry,

Research Paper ITF-018.

Feng, Y., R.I. Negrón-Juárez, and J.Q. Chambers. 2020. Remote sensing and

statistical analysis of the effects of hurricane María on the forests of Puerto

Rico. Remote Sensing of Environment 247:111940.

Fiske, I., and R. Chandler. 2011. Unmarked: An R package for fitting hierarchical

models of wildlife occurrence and abundance. Journal of statistical

software 43:1-23

Fuller, A.K., D.W. Linden, and J.A. Royle. 2016. Management decision making

for fisher populations informed by occupancy modeling. Journal of Wildlife

Management 80:794-802.

Garcia-Rivera, J.E., A.P. Marrero, and W.M. Latalladi. 2018. General Surgery
Residency Program Response Plan to Hurricane Maria in Puerto Rico. Journal
of the American College of Surgeons 227: S219.

Gesch, D.B., and D. Maune. 2007. Digital elevation model technologies and
applications: the DEM user's manual. In American Society for Photogrammetry
and Remote Sensing 2:99-118.

Gould, W.A., C. Alarcón, B. Fevold, M.E. Jiménez, S. Martinuzzi, G. Potts, ... and
E. Ventosa. 2008. The Puerto Rico Gap Analysis Project volume 1: land cover,
vertebrate species distributions, and land stewardship. Gen. Tech. Rep. IITF-
39.

Greenberg, C.H., and J.D. Lanham. 2001. Breeding bird assemblages of
hurricane-created gaps and adjacent closed canopy forest in the southern
Appalachians. Forest Ecology and Management 154:251-260.

Gregory, F.A., and A. M. Sabat. 1996. The effect of hurricane disturbance on the
fecundity of sierra palms (*Prestoea montana*). Bios. 67:135-139.

Hall, J., R. Muscarella, A. Quebbeman, G. Arellano, J. Thompson, J.K.
Zimmerman, and M. Uriarte. 2020. Hurricane-induced rainfall is a stronger
predictor of tropical forest damage in Puerto Rico than maximum wind
speeds. Scientific Reports 10:1-10.

Harris, N.L., A.E. Lugo, S. Brown, and T. Heartsill-Scalley. Luquillo Experimental
Forest: Research History and Opportunities. Experimental Forest and Range
EFR-1. Washington, DC: USDA Forest Service.

Hu, T., and R.B. Smith. 2018. The impact of Hurricane Maria on the vegetation of Dominica and Puerto Rico using multispectral remote sensing. Remote Sensing 10:827.

Hutto, R.L., S.M. Pletschet, and P. Hendricks. 1986. A fixed radius point count method for nonbreeding and breeding season use. Auk 103:593–602.

IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri, and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

Karanth, K.U., A.M. Gopalaswamy, N.S. Kumar, S. Vaidyanathan, J.D. Nichols, and D.I. MacKenzie. 2011. Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. Journal of Applied Ecology 48:1048-1056.

Kéry, M., and J.A. Royle. 2015. Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS. Academic Press, 789pp.

Knutson, T.R., J.L. McBride, J. Chan, K. Emanuel, G. Holland, C. Landsea, I. Held, J.P. Kossin, A.K. Srivastava, and M. Sugi. 2010. Tropical cyclones and climate change. Nature Geoscience 3:157–163.

Lloyd, J.D., C.C. Rimmer, and J.A. Salguero-Faría. 2019. Short-term effects of hurricanes Maria and Irma on forest birds of Puerto Rico. PLoS ONE 14(6): e0214432.

Lugo, A.E. 1994. Preservation of primary forests in the Luquillo Mountains,
Puerto Rico. Conservation Biology 8:1122-1131.

Lugo, A.E. 2008. Visible and invisible effects of hurricanes on forest ecosystems:
An international review. Austral Ecology 33:368–398.

Macfarlane, C. 2011. Classification method of mixed pixels does not affect
canopy metrics from digital images of forest overstorey. Agricultural and Forest
Meteorology 151:833-840.

MacKenzie, D.I., J.D. Nichols, G.B. Lachman, S. Droege, J.A. Royle, and C.A.
Langtimm, 2002. Estimating site occupancy rates when detection probabilities
are less than one. Ecology 83:2248-2255.

Martin, C.A. 2015. Image Analysis Primer.
github.com/cmartin/ImageAnalysisPrimer

Martin, C.A., and R. Proulx. 2016. Habitat geometry, a step toward general bird
community assembly rules in mature forests. Forest Ecology and
Management 361:163-169.

Mazerolle, M.J. 2020. Model selection and multimodel inference using the
AICcmodavg package. R package version ≥3.2.0. Available online at
http://CRAN.R-project.org/package=AICcmodavg.

Meyer, G.E., and J.C. Neto. 2008. Verification of color vegetation indices for
automated crop imaging applications. Computers and electronics in
agriculture 63:282-293.

Morin, D.J., C.B. Yackulic, J.E. Diffendorfer, D.B. Lesmeister, C.K. Nielsen, J. Reid, and E.M. Schauber. 2020. Is your ad hoc model selection strategy affecting your multimodel inference? Ecosphere 11: e02997.

Nareff, G.E., P.B. Wood, D.J. Brown, T. Fearer, J.L. Larkin, and W.M. Ford. 2019. Cerulean Warbler (*Setophaga cerulea*) response to operational silviculture in the central Appalachian region. Forest Ecology and Management 448:409-423.

Negrón-Juárez, R., D.B. Baker, H. Zeng, T.K. Henkel, and J.Q. Chambers. 2010. Assessing hurricane-induced tree mortality in US Gulf Coast Forest ecosystems. Journal of Geophysical Research: Biogeosciences 115(G4).

Odum, H.T., and R.F. Pigeon. 1970. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. Division of Technical Information, US Atomic Energy Commission.

Pickett, S.T.A., J. Kolasa, J.J. Armesto, and S.L. Collins. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos 54:129–136.

Proulx, R., and L. Parrot. 2008. Measures of structural complexity in digital images for monitoring the ecological signature of an old-growth forest ecosystem. Ecological Indicators 8:270-284.

Proulx, R., and L. Parrott. 2009. Structural complexity in digital images as an ecological indicator for monitoring forest dynamics across scale, space, and time. Ecological Indicators 9:1248-1256.

R Development Core Team. 2021. R: A language and environment for statistical computing. Available online at http://www.R-project.org. R Foundation for Statistical Computing, Vienna, Austria.

Reagan, D.P. 1991. The response of *Anolis* lizards to hurricane-induced habitat changes in a Puerto Rican rain forest. Biotropica 23:468-474.

Ricklefs, R.E. 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. The Condor 102:9-22.

Rittenhouse, C.D., A.M. Pidgeon, T.P. Albright, P.D. Culbert, M.K. Clayton, C.H. Flather, ..., and V.C. Radeloff. 2010. Avifauna response to hurricanes: Regional changes in community similarity. Global Change Biology 16:905–917.

Rivera-Milán, F.F., G.S. Boomer, and A.J. Martínez. 2014. Monitoring and modeling of population dynamics for the harvest management of scaly-naped pigeons in Puerto Rico. The Journal of Wildlife Management 78:513-521.

Rodgers, J.C., A.W. Murrah, and W.H. Cooke. 2009. The impact of Hurricane Katrina on the coastal vegetation of the Weeks Bay Reserve, Alabama from NDVI data. Estuaries and Coasts 32:496-507.

Royle, J.A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108-115.

Tejeda-Cruz, C., and W.J. Sutherland. 2005. Cloud forest bird responses to unusually severe storm damage. Biotropica 37:88–95.

Thomas, L., S.T. Buckland, E.A. Rexstad, J.L. Laake, S. Strindberg, S.L. Hedley, ... and K.P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5-14.

Thompson Baranello, J.J. 2000. Resource and population modeling of the Puerto Rican Parrot (*Amazona vittata*). University of Puerto Rico, Río Piedras, USA, p. 108.

Torres, J.A. 1992. Lepidoptera outbreaks in response to successional changes after the passage of Hurricane Hugo in Puerto Rico. Journal of Tropical Ecology 8:285-298.

Uriarte, M., J. Thompson, and J.K. Zimmerman. 2019. Hurricane María tripled stem breaks and doubled tree mortality relative to other major storms. Nature communications 10:1362.

Van Belle, G. Statistical Rules of Thumb, 2002. Willey. Available online: https://www. wiley. com/en-us/Statistical+ Rules+ of+ Thumb% 2C+ 2nd+ Edition-p-9780470144480 (accessed on 26 February 2021).

Wadsworth, F.H. 1951. Forest management in the Luquillo Mountains. I. The setting. Caribbean Forester 12:93-114.

Waide, R.B. 1991. The effect of Hurricane Hugo on bird populations in the Luquillo Experimental Forest, Puerto Rico. Biotropica 23:475-480.

Walker, L.R., Brokaw, N.V.L., Lodge, D.J., and Waide, R.B. 1991. Ecosystems, plant and animal response to hurricanes in the Caribbean. Biotropica 23:13–521.

Walker, L.R. 1991a. Summary of the effects of Caribbean hurricanes on vegetation. Biotropica 23:442-447.

Walker, L.R. 1991b. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. Biotropica 23:379-385.

Wallis, C.I., D. Paulsch, J. Zeilinger, B. Silva, G.F.C. Fernández, R. Brandl, ... and J. Bendix. 2016. Contrasting performance of Lidar and optical texture models in predicting avian diversity in a tropical mountain forest. Remote Sensing of Environment 174:223-232.

Wang, H., and C. Hall. 2004. Modeling the effects of Hurricane Hugo on spatial and temporal variation in primary productivity and soil carbon and nitrogen in the Luquillo Experimental Forest, Puerto Rico.Plant and Soil 263**:**69–84. https://doi.org/10.1023/B:PLSO.0000047719.44971.dd

Weaver, P.L., and W.A. Gould. 2013. Forest vegetation along environmental gradients in northeastern Puerto Rico. Ecological Bulletins 54:43-66.

White Jr., T.H., J.A. Collazo, F.J. Vilella, and S.A. Guerrero. 2005. Effects of Hurricane Georges oh habitat use by captive reared Hispaniolan Parrots (*Amazonia ventralis*) released in the Dominican Republic. Ornitología Neotropical 16:405-417.

Wiley, J.W., and J.M. Wunderle Jr. 1993. The effects of hurricanes on birds, with special reference to Caribbean islands. Bird Conservation International 3:319-349.

Wunderle Jr., J.M. 1995. Responses of bird populations in a Puerto Rican Forest to Hurricane Hugo: the first 18 months. Condor 97:879-896.

Wunderle Jr., J.M. 1999. Pre-and post-hurricane fruit availability: Implications for Puerto Rican parrots in the Luquillo Mountains. Caribbean Journal of Science 35:249-264.

Wunderle Jr., J.M., D.J. Lodge, and R.B. Waide. 1992. Short-term effects of Hurricane Gilbert on terrestrial bird populations on Jamaica. Auk 109:148–166.

You, C., and W.H. Petty. 1991. Effects of Hurricane Hugo on *Manilkara bidentata*, a primary tree species in the Luqillo Experimental Forest of Puerto Rico. Biotropica 23:400-406.

Zimmerman, J. K., T. E. Wood, G. González, A. Ramirez, W. L. Silver, M. Uriarte, M. R. Willig, and R.B. Waide, A. E. Lugo. 2020. Disturbance and resilience in the Luquillo Experimental Forest. Biological Conservation doi.org/10.1016/j.biocon.2020.108891

Tables

Table 1.2

Model selection results for Pearly-eyed Thrasher site occupancy probability (Ψ) in the year after Hurricane María in the Luquillo Experimental Forest. Model covariates considered were NDVI, elevation, sierra palm Forest, LAI, and MIG. Also, included were some interactions with biological relevance as well as the linear and quadratic terms for elevation and forest type. Model selection was based on Akaike's Information Criterion (AICc), number of parameters (K), the difference in AICc from the best fit model (ΔAICc), model weight (AICc Wt.). AICc is the Akaike's Information Criterion value for small sample sizes, which measures the fit of a model relative to other models. See Table 1 for code names in models.

Models	K	AICc	ΔAICc	AICc Wt.
ψ (ndvi + elev + sipa + elev:ndvi) p (date + time)	8	235.99	0	0.42
ψ (ndvi + elev + sipa + elev:ndvi) p (date + time + wind)	9	236.77	0.77	0.28
ψ (ndvi + elev + sipa + aspe + elev:ndvi + ndvi:aspe) p (date + time + wind)	11	238.43	2.44	0.12
ψ (ndvi + elev + sipa + aspe + elev:ndvi) p (date + time + wind)	10	238.72	2.72	0.11

ψ (ndvi + lai + elev + sipa + aspe + elev:ndvi + ndvi:aspe) p (date + time + wind)	12	240.44	4.45	0.05
ψ (ndvi + lai + elev + sipa + aspe + elev:ndvi + ndvi:aspe + sipa:lai) p (date + time + wind)	13	242.26	6.26	0.02
ψ (ndvi + lai + elev + sipa + aspe + elev:ndvi + ndvi:aspe + ndvi:sipa + sipa:lai) p (date + time + wind)	14	244.13	8.14	0.01

Table 2.2

Model selection results for Pearly-eyed Thrasher site abundance (λ) in the Luquillo Experimental Forest in the year after Hurricane María. Covariates considered were NDVI, elevation, sierra palm Forest, LAI, and MIG. Also included were some interactions with biological relevance. Model selection was based on Akaike's Information Criterion (AICc), number of parameters (K), the difference in AICc from the best fit model (ΔAICc), model weight (AICc Wt.). AICc is the Akaike's Information Criterion value for small sample sizes, which measures the fit of a model relative to other models. See Table 1 for code names in models.

Models	K	AICc	ΔAICc	AICc Wt.
λ (ndvi + elev + sipa + elev:ndvi) p (date + time)	8	308.4	0	0.66
λ (ndvi + elev + sipa + mig + elev:ndvi + elev:mig) p (date + time)	10	310.83	2.43	0.2
λ (ndvi + lai + elev + sipa + mig + elev:ndvi + elev:mig) p (date + time)	11	312.42	4.02	0.09
λ (ndvi + lai + elev + sipa + mig + elev:ndvi + elev:mig + ndvi:sipa) p (date + time + prec)	13	314.07	5.66	0.04

λ (ndvi + lai + elev + sipa + mig +

elev:ndvi + elev:mig + ndvi:sipa +

sipa:lai) p (date + time + wind +

prec)   15   316.51   8.1   0.01

Figures

Figure 1.2

Map of the Luquillo Experimental Forest and its location in NE Puerto Rico (grey area in the inserted map). The black circles represent all sites sampled. Different colors represent differences in elevation (m a.s.l.).
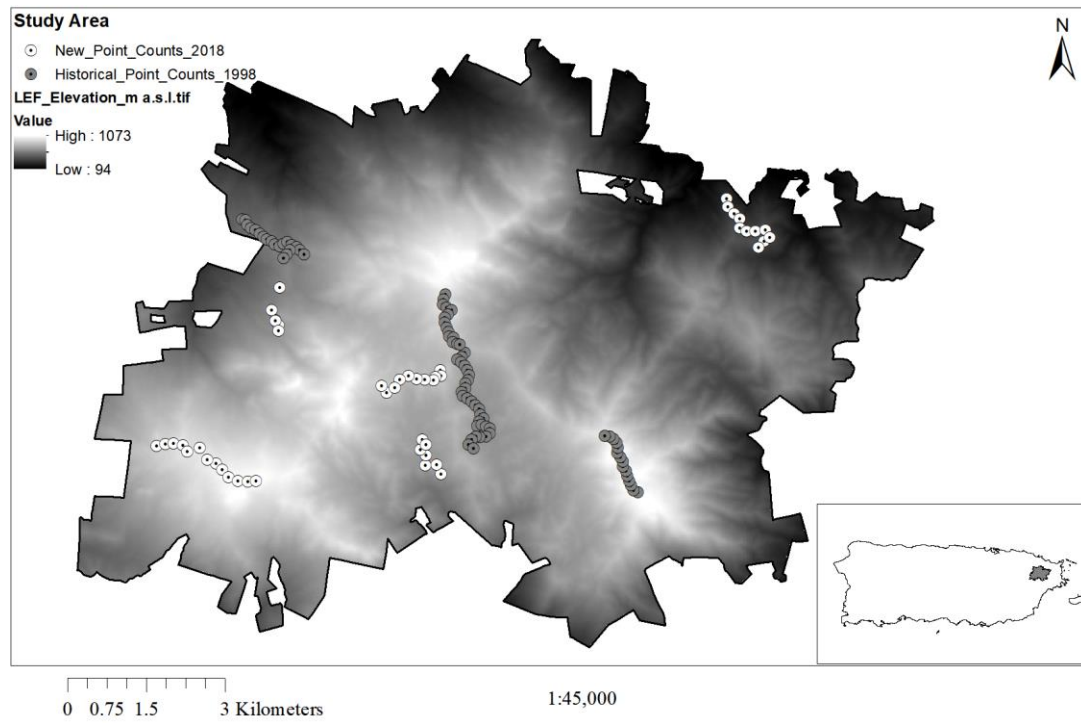
Figure 2.2

Pearly-eyed Thrasher predicted site occupancy probability (A) and abundance (B) values across percent sierra palm forest cover in the Luquillo Experimental Forest in the year (2018) after Hurricane María.
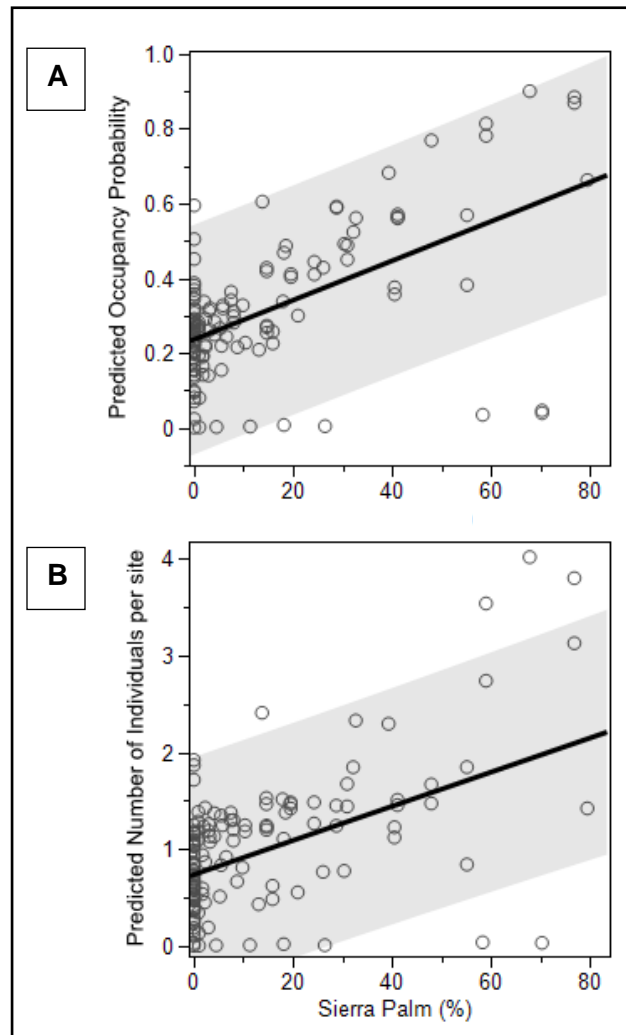
Figure 3.2

Relationship between NDVI values and the elevational gradient in the Luquillo

Experimental Forest in 2018 after Hurricane Maria. Dots present the NDVI values

for each site, the line depicts the mean, and the gray area shows the predicted

intervals (PI).
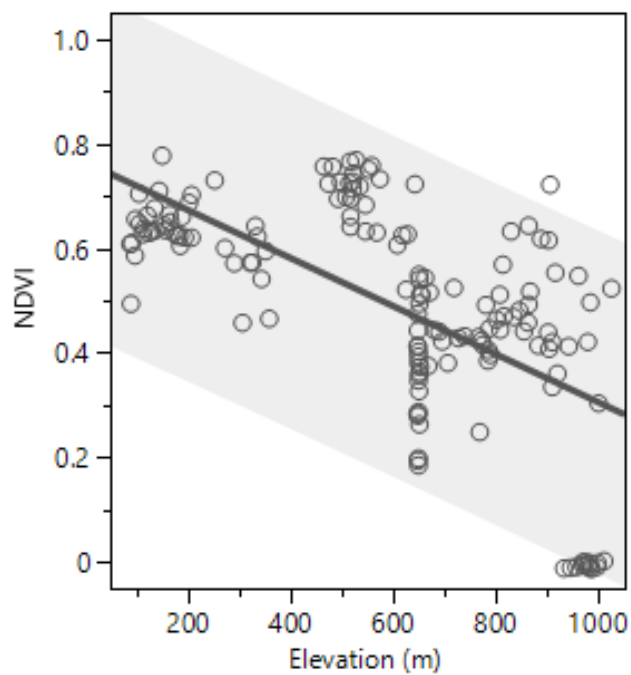
Figure 4.2

Pearly-eyed Thrasher predicted site occupancy probability (A) and abundance

(B) values across the elevation gradient in the Luquillo Experimental Forest in the

year after Hurricane Maria. Red represent low NDVI values (0 – 0.4) and green

represent high NDVI values (0.4 – 0.8). Sites with high NDVI values indicate less

storm damage to vegetation than sites with low NDVI values.
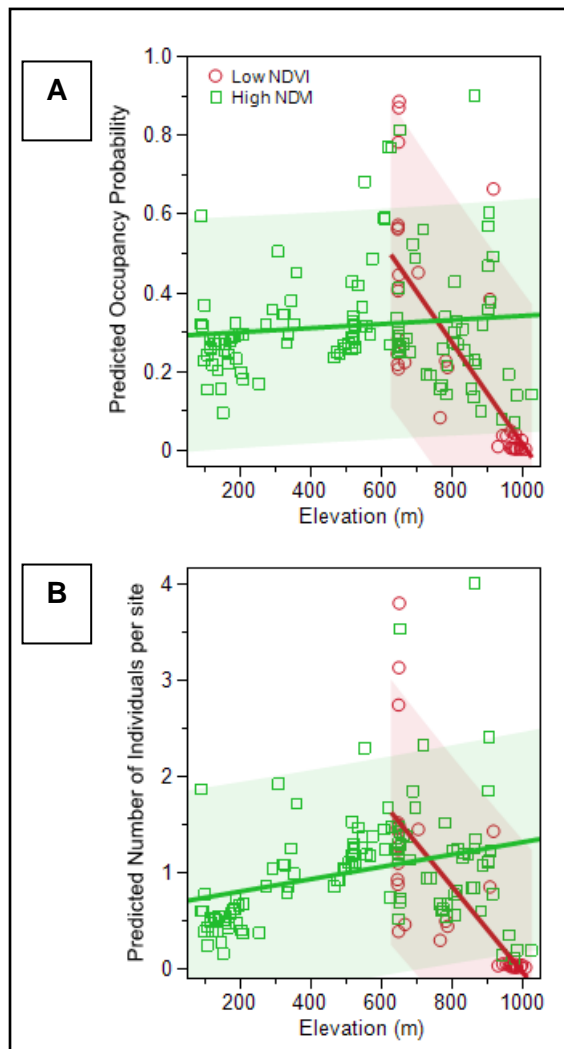
Table S1.2

Camara settings

Exposure	Variable
Focal Length	18.0 mm
Aperture	f/6.3 mm
ISO	800
Resolution	2592 X 1728
Metering mode	Centre-weighted average
Focus	Automatic
Image stabilization	ON
Compression	JPEG high-quality
White balance mode	Daylight
Exposure mode	Aperture priority
Depth of field (DF)	2.28 m – infinity
Focus Distance	15.0 m

Table S2.2

Pairwise correlation of all covariates for abundance and occupancy sub-models.

Variable	by Variable	Correlation	P-Value
NDVI	Distance_road	0.0716	0.3715
Canopy_cover	Distance_road	-0.1768	0.0263*
Canopy_cover	NDVI	-0.3671	<.0001*
Slope	Distance_road	0.2873	0.0003*
Slope	NDVI	0.0662	0.4088
Slope	Canopy_cover	-0.1274	0.1108
Elevation	Distance_road	0.4100	<.0001*
Elevation	NDVI	-0.6235	<.0001*
Elevation	Canopy_cover	0.1189	0.1369
Elevation	Slope	0.0386	0.6301
Aspect	Distance_road	0.0859	0.2834
Aspect	NDVI	-0.2228	0.0049*
Aspect	Canopy_cover	0.1348	0.0913
Aspect	Slope	0.0045	0.9555
Aspect	Elevation	0.1842	0.0205*
Tabonuco	Distance_road	-0.3394	<.0001*
Tabonuco	NDVI	0.6484	<.0001*
Tabonuco	Canopy_cover	-0.2514	0.0014*
Tabonuco	Slope	0.0123	0.8782

Variable	by Variable	Correlation	P-Value
Tabonuco	Elevation	-0.8474	<.0001*
Tabonuco	Aspect	-0.1210	0.1298
Palo_Colorado	Distance_road	0.4483	<.0001*
Palo_Colorado	NDVI	-0.2719	0.0005*
Palo_Colorado	Canopy_cover	0.2090	0.0084*
Palo_Colorado	Slope	0.0279	0.7275
Palo_Colorado	Elevation	0.5904	<.0001*
Palo_Colorado	Aspect	-0.0179	0.8237
Palo_Colorado	Tabonuco	-0.7858	<.0001*
Sierra_Palm	Distance_road	-0.0269	0.7375
Sierra_Palm	NDVI	-0.3684	<.0001*
Sierra_Palm	Canopy_cover	0.1300	0.1035
Sierra_Palm	Slope	-0.0227	0.7769
Sierra_Palm	Elevation	0.3810	<.0001*
Sierra_Palm	Aspect	0.1855	0.0196*
Sierra_Palm	Tabonuco	-0.4315	<.0001*
Sierra_Palm	Palo_Colorado	-0.0112	0.8888
Elfin_forest	Distance_road	-0.0913	0.2540
Elfin_forest	NDVI	-0.6163	<.0001*
Elfin_forest	Canopy_cover	0.0408	0.6105
Elfin_forest	Slope	-0.0290	0.7180
Elfin_forest	Elevation	0.4528	<.0001*

Variable	by Variable	Correlation	P-Value
Elfin_forest	Aspect	0.1844	0.0204*
Elfin_forest	Tabonuco	-0.2960	0.0002*
Elfin_forest	Palo Colorado	-0.1849	0.0200*
Elfin_forest	Sierra_Palm	0.0928	0.2462
MIG	Distance_road	-0.1834	0.0211*
MIG	NDVI	0.1184	0.1384
MIG	Canopy_cover	0.0707	0.3772
MIG	Slope	-0.0841	0.2935
MIG	Elevation	-0.1384	0.0828
MIG	Aspect	-0.1713	0.0314*
MIG	Tabonuco	0.0345	0.6670
MIG	Palo_Colorado	0.0866	0.2794
MIG	Sierra_Palm	-0.1596	0.0452*
MIG	Elfin_forest	-0.1320	0.0984
ExG-ExR	Distance_road	-0.1009	0.2073
ExG-ExR	NDVI	0.4710	<.0001*
ExG-ExR	Canopy_cover	-0.1968	0.0132*
ExG-ExR	Slope	0.1968	0.0132*
ExG-ExR	Elevation	-0.4704	<.0001*
ExG-ExR	Aspect	0.0079	0.9218
ExG-ExR	Tabonuco	0.4994	<.0001*
ExG-ExR	Palo_Colorado	-0.3749	<.0001*

Variable	by Variable	Correlation	P-Value
ExG-ExR	Sierra_Palm	-0.1032	0.1968
ExG-ExR	Elfin_forest	-0.3140	<.0001*
ExG-ExR	MIG	-0.1100	0.1688
LAI	Distance_road	0.1516	0.0573
LAI	NDVI	0.4773	<.0001*
LAI	Canopy_cover	-0.2338	0.0031*
LAI	Slope	0.4093	<.0001*
LAI	Elevation	-0.3050	<.0001*
LAI	Aspect	0.0110	0.8910
LAI	Tabonuco	0.3350	<.0001*
LAI	Palo_Colorado	-0.1652	0.0380*
LAI	Sierra_Palm	-0.0785	0.3271
LAI	Elfin_forest	-0.3454	<.0001*
LAI	MIG	-0.0843	0.2922
LAI	ExG-ExR	0.6507	<.0001*

Table S3.2

Forward stepwise selection for detection probability in single season occupancy model.

Models	K	AICc	ΔAICc	AICcWt
ψ(.) p (date + wind + time)	5	242.67	0	0.25
ψ(.) p (date + wind)	4	243.09	0.41	0.21
ψ(.) p (date)	3	243.8	1.13	0.14
ψ(.) p (date + time)	4	244	1.33	0.13
ψ(.) p (wind)	3	244.6	1.92	0.1
ψ(.) p (time)	3	245.73	3.06	0.05
ψ(.) p (.)	2	245.92	3.25	0.05
ψ(.) p (precipitation)	3	247.16	4.49	0.03
ψ(.) p (ndvi)	3	247.59	4.92	0.02
ψ(.) p (cloud)	3	247.82	5.15	0.02

Table S4.2

Forward stepwise selection for detection probability in single season *N*-mixture model.

Models	K	AICc	ΔAICc	AICcWt
p (date + time + wind + precipitation)	6	315.51	0	0.22
p (date + time + wind)	5	315.82	0.31	0.19
p (date + wind)	4	317.08	1.57	0.1
p (date + time + precipitation)	5	317.38	1.88	0.09
p (date + time + wind + ndvi)	6	317.45	1.94	0.08
p (date + time)	4	317.84	2.34	0.07
p (date + precipitation)	4	318.08	2.58	0.06
p (date)	3	318.35	2.85	0.05
p (date + time + ndvi)	5	318.62	3.11	0.05
p (ndvi + date)	4	319.37	3.86	0.03
p (date + cloud)	4	320.22	4.72	0.02
p (wind)	3	321.66	6.15	0.01
p (time)	3	322.98	7.47	0.01
p (.)	2	323.93	8.43	0
p (ndvi)	3	324.82	9.31	0
p (cloud)	3	325.42	9.91	0
p (precipitation)	3	325.6	10.09	0

Table S5.2

Covariate selection for occupancy probability sub-model in single season
occupancy model.

Models	K	AICc	ΔAICc	AICcWt
Ψ (sierra palm:lai)	5	239.3	0	0.35
Ψ (ndvi:sierra palm)	5	240.42	1.12	0.2
Ψ (ndvi:aspect)	5	241.84	2.54	0.1
Ψ (sierra palm)	3	242.2	2.89	0.08
Ψ (ndvi:elevation)	5	242.33	3.03	0.08
Ψ (lai)	3	244.4	5.1	0.03
Ψ (.)	2	245.92	6.62	0.01
Ψ (ndvi:lai)	5	246.64	7.34	0.01
Ψ (ndvi)	3	246.74	7.44	0.01
Ψ (ndvi:mig)	5	246.87	7.57	0.01
Ψ (exg_exr)	3	247.17	7.86	0.01
Ψ (canopy.height)	3	247.22	7.92	0.01
Ψ (elevation:lai)	5	247.55	8.25	0.01
Ψ (mig)	3	247.59	8.29	0.01
Ψ (slope)	3	247.6	8.3	0.01
Ψ (elevation)	3	247.79	8.49	0.01
Ψ (aspect)	3	247.93	8.63	0
Ψ (distance.road)	3	247.93	8.63	0

Ψ (ndvi:canopy.height)	5	248.24	8.93	0
Ψ (ndvi:slope)	5	248.89	9.59	0
Ψ (ndvi:exg_exr)	5	248.96	9.65	0

Table S6.2

Covariate selection for abundance sub-model in single season N-mixture model.

Models	K	AICc	ΔAICc	AICcWt
λ (ndvi:elevation)	5	315.7	0	0.67
λ (ndvi:sierra palm)	5	319.77	4.07	0.09
λ (sierra palm:lai)	5	320.18	4.48	0.07
λ (lai)	3	321.42	5.72	0.04
λ (sierra palm)	3	322.21	6.5	0.03
λ (ndvi:mig)	5	322.77	7.07	0.02
λ (.)	2	323.93	8.23	0.01
λ (exg_exr)	3	324.13	8.43	0.01
λ (ndvi)	3	324.3	8.6	0.01
λ (ndvi:lai)	5	324.33	8.63	0.01
λ (ndvi:aspect)	5	324.89	9.19	0.01
λ (sierra palm:slope)	5	325.16	9.46	0.01
λ (canopy.height)	3	325.66	9.96	0
λ (mig)	3	325.76	10.06	0
λ (elevation)	3	325.91	10.21	0
λ (slope)	3	325.91	10.21	0
λ (distance.road)	3	325.91	10.21	0
λ (aspect)	3	325.93	10.23	0
λ (ndvi:exg_exr)	5	325.93	10.23	0

λ (ndvi:canopy.height)	5	326.06	10.35	0
λ (sierra palm:canopy.height)	5	326.13	10.43	0
λ (ndvi:slope)	5	327.38	11.68	0

Table S7.2

Detection probability beta estimates, standard errors, and p-values from the top

ranked model (see Table 1.2 and 2.2).

Model Covariates	β Estimate	SE	P values
Intercept	-2.27	0.67	0.001
date	-0.41	0.19	0.030
time	-0.27	0.17	0.108

Table S8.2

Predicted values, standard errors, and 95% confidence intervals (CI) from the top

ranked model (see Table 1.2 and 2.2).

Visits	Predicted Detection (*p*)	SE	Lower	Upper
1	0.10	0.06	0.03	0.30
2	0.10	0.06	0.03	0.30
3	0.12	0.08	0.03	0.35

Figure S1.2

Photo description based on the inclination of the camara, 0° for mean information gain and greenness index, and 45° for the leaf area index.